

ECOLOGICAL EFFECTS OF DISEASE- INDUCED APEX PREDATOR DECLINE

The Tasmanian Devil and Devil Facial Tumour Disease



Tracey Anne Hollings, MConBio, BSc

School of Zoology

University of Tasmania

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

April, 2013



Declarations by the Author

Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright

Signed:

Tracey Anne Hollings

Date: April 2013

Authority of Access

This thesis may be made available for loan and limited copying and communication in accordance with the Copyright Act 1968

Signed:

Tracey Anne Hollings

Date: April 2013

Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australia codes on animal experimentation. Animal ethics permits were obtained from the University of Tasmania Animal Ethics Committee for all aspects of the project where experiments involved live animals.

Signed:

Tracey Anne Hollings

Date: April 2013

Statement of Co-Authorship and Thesis Contributions

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Tracey Hollings	University of Tasmania, Hobart, Australia
Hamish McCallum	Griffith University, Brisbane, Australia
Menna Jones	University of Tasmania, Hobart, Australia
Nick Mooney	Independent biologist, Hobart, Australia
Greg Hocking	Department of Primary Industries, Parks, Water and the Environment (DPIPWE), Hobart, Australia

Submitted publications forming part of this thesis

Hollings, T.A., Jones, M.E., Hocking, G., Mooney, N., McCallum, H.I. Trophic cascades following the disease-induced decline of an apex predator, the Tasmanian devil. In review. (Chapter Two)

Hollings, T.A., Jones, M.E., Mooney, N., McCallum, H.I. 2013. Wildlife disease ecology in changing landscapes: the mesopredator release and toxoplasmosis. *International Journal of Parasitology: Parasites and Wildlife* 2: 110-118 (Chapter Five)

Publications in preparation forming part of this thesis

Hollings, T.A., Jones, M.E., Mooney, N., McCallum, H.I. Disease-induced decline of an apex predator drives invasive dominated states and threatens biodiversity. In preparation. (Chapter Three)

Hollings, T.A., McCallum, H.I., Mooney, N., Jones, M.E. Changes in risk-sensitive behaviour of prey following disease-induced decline of an apex predator, the Tasmanian devil. In preparation. (Chapter Four)

Author roles

Candidate contributed to ideas, designed and undertook all fieldwork, conducted the analyses and wrote the manuscripts.

Menna Jones and Hamish McCallum contributed to ideas, aided with analyses and edited the manuscripts.

Nick Mooney contributed to ideas and edited the manuscripts

Greg Hocking designed, instigated and conducted much of the fieldwork for the longitudinal study in chapter two.

We the undersigned agree with the above stated “proportion of work undertaken” for each of the above submitted peer-reviewed manuscripts contributing to this thesis

Hamish McCallum
(Primary Supervisor)

Date: April 2013

Elissa Cameron
(Head of School)

Date: April 2013

Acknowledgements

A project such as this would never be possible without the substantial support and guidance from a wide variety of people and organisations. I extend my sincere gratitude and appreciation to everyone who has assisted me and the research undertaken throughout this project.

First and foremost I would like to thank my supervisors, Prof. Hamish McCallum, Dr Menna Jones and Mr Nick Mooney, without whom this project would never have gotten off the ground. I am sincerely grateful to you for giving me the opportunity to carry out this research thesis, as well as allowing me the freedom to pursue my own ideas and directions. Your guidance, wisdom, patience and enthusiasm were pivotal in the execution and completion of this work.

I would like to thank the several funding bodies which provided financial contributions which made this predominantly field based project possible: the Eric Guiler Tasmanian Devil Research Fund, the Holsworth Wildlife Research Endowment, Ecological Society of Australia and the CRC for Forestry. I was the recipient of an Australian Government Postgraduate Award and Qantas Tasmanian Devil Research Scholarship, and I would like to acknowledge this significant contribution to my personal circumstances which allowed me to pursue this incredible opportunity.

Working at numerous locations across the Tasmanian state I came in to contact with many amazing and wonderful folk. I would like to particularly mention and gratefully thank all the staff at Forestry Tasmania who helped me in some way and the Parks and Wildlife Rangers

for their help and advice on site. I would like to make special mention of AJ and Judy at Narawntapu National Park for all their assistance over the years. I hope to be back one day soon to share another cold one. Also, a whole-hearted thank you to Geoff King who allowed me to conduct surveys on his land, helped me navigate the north-west and always invited us to his “devil den” for some late night devil viewing over a bottle of red.

I would like to thank all the staff at the Department of Primary Industries, Parks, Water and the Environment, including those in the “Save the Tasmanian Devil Program”: Andrew Sharman, Chris Boland, Sam Fox, Greg Hocking, Kris Carlyon, Drew Lee and Michael Driessen. Your assistance and guidance over the years was sincerely appreciated.

Without the help and assistance of Forestry Tasmania and their contract shooters the disease ecology aspect of this project could not have transpired. Thank you especially to Wade, Anthony, Greg and David for allowing me to accompany them during their work or collecting samples for me when necessary. Thank you also to Pat Statham and Sarah Peck from Mt Pleasant Animal Health laboratories in Launceston for teaching me the methodology and providing answers to all those curly questions.

To my many incredible volunteers, I want to thank you for making my field work so enjoyable and being a source of entertainment through the seemingly endless monotony of pulling off hair tube tape. I am grateful to you all for taking the time to join me for extended periods away and for your interest and eagerness to assist.

I would like to also thank the entire UTAS School of Zoology staff, but particularly to Richard Holmes who had the imagination and talent to make the un-makeable; to Wayne Kelly for all manner of IT and lab support; Barry Rumbold for managing all things financial; Adam

Stephens as the master of car negotiations; Felicity Wilkinson the heart and soul of zoology and Erik Wapstra as our very friendly and efficient postgraduate co-ordinator. Also, my sincere appreciation and admiration goes to Professor Leon Barmuta, Dr Nick Beeton and Shannon Troy for their patience and assistance with my seemingly endless queries of R and statistics.

To my fellow post-grads in the UTAS School of Zoology: Ryan, Elias, Lisa, Gemma, Rach, Laura, Nick, Shelly, Anna, Rodrigo, and Jo, who have shared the daily slog, I want to thank and acknowledge you for providing much needed respite with conversations in the corridors, encouragement over cake and the all important Friday night beverage. I also take this opportunity to provide my sincerest thanks and gratitude to Shannon, field work guru, ear to chew, ideas woman and very dear friend. I couldn't have done it without you.

I am indebted to my very dear friends Corrie for our pursuit of the best butter chicken Hobart had to offer, Dr FiFi Poke for teaching me the value of a Friday night wine for remembering life outside the thesis, and to Prue, Narissa and Christian for good times and lots of laughter. To the Cartela St Crew Ryan, Elias and Judith, my best friends and awesome housemates, you made it a pleasure to come home at night. I miss you already. And our view.

Lastly but certainly not least I want to sincerely thank my family. Your unconditional love, support and encouragement has been unwavering and your commitment to my happiness extends far beyond what I could ever expect. You came on my field adventures with me and got to experience firsthand the work that I love so much, despite being elbow deep in mutton bird oil and kiwi-bred snake phobias. Words cannot express my appreciation and gratitude for

everything you have done and continue to do for me, I am truly blessed to have such an amazing family.

My beautiful partner Cam, we have taken this journey together, we have both learnt so much and come so far. Your understanding, commitment and encouragement throughout this PhD have been truly incredible. Thank you for being my rock and my best friend.

Abstract

The global extirpation of the world's apex predator fauna is consistently highlighting their important functional role in preserving biodiversity and maintaining ecosystem resilience. Apex predator declines and extinctions are promoting more invasive and homogenised ecosystem states, linked with secondary species extinctions, changes to community composition, and redefined carnivore guilds. In taxonomically and geographically diverse ecosystems devoid of apex predators similar general patterns expressed in community dynamics are emerging, such as mesopredator release, yet the magnitude and significance of the effects are driven by their context.

The Tasmanian devil (*Sarcophilus harrisii*) is the largest extant marsupial carnivore and is facing the real threat of disease induced extinction in the wild from a consistently fatal transmissible cancer, devil facial tumour disease (DFTD). The devil is now effectively the apex mammalian predator in Tasmanian ecosystems following the extinction of the thylacine (*Thylacinus cynocephalus*) but DFTD is threatening its ecological role in the environment. Since the disease arose in the early to mid 1990s devil populations have suffered declines in excess of 95% in long-term disease areas, and it has infected more than 75% of their current geographic range. Tasmania retains the most intact guild of marsupial carnivores in Australia and maintains healthy populations of many native mammal and bird species that are extinct or threatened on mainland Australia. The loss of Tasmanian devils over large tracts of Tasmania is of tremendous conservation concern for native biodiversity and community resilience.

This study provides the first assessment of the ecosystem effects of Tasmanian devil decline and aims to determine overarching effects of the loss of an ecologically functional devil population on terrestrial mammalian fauna. Within the scope of this thesis, broad concepts encompassing abundance, behaviour and disease ecology of native and introduced species are assessed within four discrete projects. I utilised complimentary approaches with the benefit of this unique large scale natural experiment to assess common theories as well as considering less widely examined concepts which may be pertinent to global apex predator demise. First, using a state-wide spotlighting database which pre-dates DFTD by more than a decade, I evaluated the mesopredator release hypothesis (MRH) and the extent to which mesopredators are regulated by top-down or bottom-up environmental processes. Second, I conducted a rapid snapshot survey across a large spatial extent encompassing different devil densities to assess changes to community composition, invasive system states and the cascading effects of mesopredator release on populations of their prey. Third, I measured risk-sensitive behaviour of the common brushtail possum, a species regularly preyed upon by Tasmanian devils, employing a ‘giving up densities’ approach across a DFTD arrival gradient, which represents a proxy for devil population decline over time. Finally, following the evidence for mesopredator release of feral cats, I assessed whether there was potential for increased disease transmission of *Toxoplasma gondii*, a parasite whose only known definitive hosts are members of the Felid family but that can infect all warm-blooded mammals.

This study provided several lines of evidence for a shifting ecosystem state and increasing threats to the persistence of native biodiversity in response to declining devil populations. Less diverse communities and a strong tendency towards more invasive system states were characteristic of areas with long-term devil decline. Native and introduced mammals

responded differently to devil decline, and the direction of the response for species of each origin was consistent across different trophic levels. I found strong evidence for mesopredator release of the invasive feral cat (*Felis catus*) in response to devil decline and a concomitant decline and changing activity times in the much smaller native eastern quoll (*Dasyurus viverrinus*), suggesting that they may be indirectly protected by devils. Despite the comparable size and prey range of native spotted-tailed quolls (*Dasyurus maculatus*) to feral cats, there was no evidence of a similar response, notwithstanding some evidence for different activity times across different devil densities. The magnitude of the responses of mesopredators to declining devil populations was significantly affected by environmental variables. In anthropogenically dominated landscapes bottom-up control appears to be the principal regulating force, and in less disturbed areas top-down control is stronger. There was evidence for an increasingly invasive state, represented by a significantly higher proportion of activity of feral cats and introduced small mammals, which appeared to be affecting native prey species. Small- and medium-sized native species within the prey size range of large mesopredators showed population declines analogous to the declines observed in devil populations and also evidence for increased predation pressure, indicating that apex predator loss in Tasmania is threatening native biodiversity.

There was evidence of behavioural responses in prey species to the decline in devil numbers. Using the giving up densities approach, I found evidence that the predominantly arboreal brushtail possum (*Trichosurus vulpecula*), a common prey item of devils, has changed its anti-predator behaviours and has increased its ground foraging activity in response to declining devil populations, whilst maintaining vigilant behaviours appropriate for the avoidance of

other predator species. Behavioural responses have the potential to initiate a trophic cascade if changes in behaviour translate into increased fitness and reproductive output.

Some native species are at risk from higher feral cat densities not only from increasing predation pressure but also from potentially amplified transmission of the *Toxoplasma* parasite. Australian native marsupials may be particularly susceptible to acute *Toxoplasma*, a consequence likely attributable to a lack of co-evolution. I found tentative support for higher prevalence rates in areas with higher cat densities and also a strong link to increased susceptibility in native species at higher trophic levels. There was also some suggestion for reduced behavioural reactions in infected individuals, with the potential to increase predation rates. This was among the first research that has investigated changing disease dynamics in response to mesopredator release, and represents an important and novel step towards more wide-ranging research of the effects of apex predator loss on biodiversity.

The combined results, derived from empirical approaches, provide compelling evidence that diverse and complex changes are occurring in Tasmania's fauna communities following apex predator decline. The evidence is indicative of extensive and far-reaching consequences in the Tasmanian ecosystem, threatening native biodiversity and promoting alternative ecosystem states. The lessons learned from applying existing community ecology theories and approaches to this unique large scale natural experiment are applicable to other ecosystems confronted with apex predator loss and highlight the importance of a multifaceted and comprehensive approach to apex predator studies.

Keywords

Tasmanian devils; DFTD; mesopredator release; giving up densities; top-down; bottom-up; trophic cascade; feral cat; Australia; Tasmania; toxoplasmosis; quoll; spotlighting; camera trapping; disease ecology; common brushtail possum; anti-predator behaviour

Table of Contents

DECLARATIONS BY THE AUTHOR	II
Declaration of Originality	ii
Authority of Access	ii
Statement of Ethical Conduct	iii
STATEMENT OF CO-AUTHORSHIP AND THESIS CONTRIBUTIONS	IV
ACKNOWLEDGEMENTS	VI
ABSTRACT	X
KEYWORDS	XIV
TABLE OF CONTENTS	XV
LIST OF FIGURES.....	XVIII
LIST OF TABLES.....	XX
CHAPTER 1: GENERAL INTRODUCTION	1
1.1 The ecosystem effects of apex predator loss in a global context	2
1.2 The vulnerability of large mammals and apex predators in particular to extinction	6
1.3 Disease in wildlife and apex carnivores	8
1.4 The Tasmanian Devil and DFTD	10
1.5 The Tasmanian ecosystem.....	16
1.6 Predictions for Tasmania based on lessons learned globally	19
1.7 Thesis context and aims.....	22
1.8 Thesis structure.....	24
CHAPTER 2: TROPHIC CASCADES FOLLOWING THE DISEASE-INDUCED DECLINE OF AN APEX PREDATOR	28
2.1 ABSTRACT	29
2.2 KEY WORDS	30
2.3 INTRODUCTION	31
2.4 METHODS	35
2.4.1 Data collection	35
2.4.2 Data organisation.....	36
2.4.3 Statistical analysis	39

2.5	RESULTS	42
2.5.1	<i>Population changes associated with DFTD arrival</i>	42
2.5.2	<i>Bottom-up and top-down influences</i>	49
2.6	DISCUSSION.....	52
2.7	ACKNOWLEDGEMENTS	57
CHAPTER 3: DISEASE-INDUCED DECLINE OF AN APEX PREDATOR DRIVES INVASIVE-DOMINATED STATES AND THREATENS BIODIVERSITY		58
3.1	ABSTRACT	59
3.2	KEY WORDS	60
3.3	INTRODUCTION	61
3.4	METHODS	65
3.4.1	<i>DFTD arrival regions and years since disease arrival</i>	65
3.4.2	<i>Site selection.....</i>	67
3.4.3	<i>Data collection methods.....</i>	67
3.4.4	<i>Species aggregations and exclusions for analyses</i>	69
3.4.5	<i>Statistical analysis</i>	71
3.5	RESULTS	76
3.5.1	<i>Community composition</i>	76
3.5.2	<i>Invasive species community composition.....</i>	78
3.5.3	<i>Mesopredator activity index and relative abundance of prey species</i>	80
3.5.4	<i>Mesopredator activity times</i>	86
3.6	DISCUSSION.....	91
3.7	ACKNOWLEDGEMENTS	99
CHAPTER 4: CHANGES IN RISK-SENSITIVE BEHAVIOUR OF PREY FOLLOWING DISEASE-INDUCED DECLINE OF AN APEX PREDATOR.....		100
4.1	ABSTRACT	101
4.2	KEY WORDS	102
4.3	INTRODUCTION	103
4.4	METHODS	108
4.4.1	<i>DFTD arrival times and site selection.....</i>	108
4.4.2	<i>Index of terrestrial possum and devil activity.....</i>	109
4.4.3	<i>Giving up densities</i>	109
4.4.4	<i>Statistical analysis</i>	112
4.5	RESULTS	116
4.5.1	<i>Terrestrial possum and devil activity.....</i>	116
4.5.2	<i>Time to find food patches.....</i>	118

4.5.3	<i>Giving up densities</i>	120
4.6	DISCUSSION.....	123
4.7	ACKNOWLEDGEMENTS	129
CHAPTER 5: WILDLIFE DISEASE ECOLOGY IN CHANGING LANDSCAPES: MESOPREDATOR RELEASE AND TOXOPLASMOSIS.....		130
5.1	ABSTRACT	131
5.2	KEY WORDS	132
5.3	INTRODUCTION	133
5.4	METHODS	137
5.4.1	<i>Blood Samples</i>	137
5.4.2	<i>Testing for T. gondii</i>	138
5.4.3	<i>Approximating cat density</i>	139
5.4.4	<i>Statistical Analysis</i>	143
5.5	RESULTS	145
5.5.1	<i>Seroprevalance of T. gondii</i>	145
5.5.2	<i>Trophic level differences</i>	147
5.6	DISCUSSION.....	149
5.7	ACKNOWLEDGEMENTS	155
CHAPTER 6: GENERAL DISCUSSION		156
6.1	Introduction	157
6.2	The ecological effects of DFTD and their significance for global apex predator loss	158
6.3	Does the loss of apex predators lead to increasingly invasive states, declining ecosystem complexity and reduced resilience of biodiversity?.....	161
6.4	Do environmental factors and predator guild dynamics influence the strength of interactions and the magnitude of responses to apex predator loss?	163
6.5	Ecological restoration	166
6.6	Challenges of studying large apex predators	170
6.7	Directions for future research	171
6.8	Concluding remarks.....	176
REFERENCES		178

List of Figures

FIGURE 1.1: <i>Two separate devils infected with DFTD, both in an advanced stage. DFTD is named after the gross lesions which often form around the face and neck.</i>	12
FIGURE 1.2: <i>Map of sites where DFTD has been confirmed prior to 2012. Devil decline is highest in areas of long-term disease in the eastern part of the state. Devils are not present on offshore islands. (Data from Department of Primary Industries, Parks, Water and Environment; Hawkins et al, 2006).</i>	15
FIGURE 1.3: <i>Thesis structure outlining the questions addressed for species at each trophic level. Arrows represent the species relationships assessed and direction of those relationships</i>	26
FIGURE 2.1: <i>Map of Tasmania showing individual spotlight survey transects divided into four regions based on the year of DFTD arrival. Brackets indicate the range of dates for confirmed DFTD arrival in each region.</i>	38
FIGURE 2.2: <i>Annual rainfall totals for each DFTD arrival region. Dashed lines indicate the mean annual rainfall derived for each region (1961-1990) from the Australian Bureau of Meteorology.</i>	41
FIGURE 2.3: <i>Results of GAM models for top order carnivore species within each DFTD region. Vertical lines represent period of disease arrival. Shaded areas are 95% confidence intervals for GAM models.</i>	44
FIGURE 2.4: <i>Results for the GAM models for devil and mesopredator prey species within each DFTD region.</i>	45
FIGURE 2.5: <i>Graphs represent the best GLM model outputs for all top order carnivore species except feral cats where the second best model was used (Table 2.1a) to illustrate DFTD arrival effects. The best model for feral cats, the linear model, was not significantly different from models containing a DFTD arrival variable. Vertical lines represent the period of disease arrival. Shaded regions are the 95% confidence intervals. Points represent the actual values.</i>	47
FIGURE 3.1: <i>Field sites, categorised into vegetation type, arranged into three DFTD arrival regions: early DFTD presence; mid-term DFTD presence; and DFTD absent (disease free).</i>	66
FIGURE 3.2: <i>Photo of camera set up with bait canister</i>	69
FIGURE 3.3: <i>Non-metric multidimensional plot for species compositions across the three DFTD regions of early disease, mid-term disease and regions which are currently disease free. Results for the permutational multivariate analysis are shown inside the plot for each vegetation type.</i>	77

FIGURE 3.4: <i>The percentage of positive hair traps which were identified as an introduced species, based on mesopredator and their prey species. Error bars represent the 95% binomial confidence intervals. C = coastal woodland scrub, D = Dry eucalypt forest, W = Mature wet eucalypt forest, WR = Wet eucalypt regenerated forest.....</i>	78
FIGURE 3.5: <i>Number of positive hair traps as a measure of activity index or relative abundance of species in different habitat types, across the range of DFTD arrival times. C = coastal woodland scrub, D = Dry eucalypt forest, W = Mature wet eucalypt forest, WR = Wet eucalypt regenerated forest. Medium mammals = southern brown bandicoot, eastern barred bandicoot and long-nosed potoroo; Native mammals = swamp rat and long-tail mouse; Introduced small mammals = black rat</i>	82
FIGURE 3.6: <i>Activity time plots for native mesopredators and devils. The data for time of activity was transformed to the number of hours since twilight with sunrise and sunset set at zero. Night time had negative values and day time positive values.</i>	90
FIGURE 4.1: <i>Field site locations for GUD experiment and hair traps. Circles enclose the sites for the three predation risk regions of low (early disease), medium (mid-term disease) and high (disease free). Sites are limited to the northern half of the island state. Predation risk represents the projected level of predation as interpolated from DFTD arrival times and corresponding devil decline.</i>	115
FIGURE 4.2: <i>Number of hits of hair traps by devils and possums as an index measure of activity in dry eucalypt forest and coastal woodland scrub habitat types across sites with a range of DFTD arrival times.</i>	117
FIGURE 4.3: <i>Kaplan-Meier estimates of the survival function for the proportion of feeding patches not found by possums over the four nights they were deployed.</i>	120
FIGURE 5.1: <i>Map of Tasmania showing average cat densities from individual spotlighting districts over 8 years and blood collection sites for the Tasmanian pademelon. Sites positive for T. gondii infection are those where at least one sample tested positive to IgG antibodies. Negative sites are those where no evidence of exposure to T. gondii was found in any sample.</i>	140
FIGURE 5.2: <i>Map of Tasmania showing blood collection sites for the three native carnivore species and the introduced feral cat. Places identified are those referred to in the text.</i>	142
FIGURE 5.3: <i>Prevalence of IgG antibodies of Tasmanian mammals to toxoplasmosis by trophic level; n represents the total number of samples tested. Standard error bars are shown.</i>	148

List of Tables

TABLE 2.1: *Results of GLM analyses showing $\Delta AICc$ and model weight (w_i) for the top candidate models for top order carnivores for the a) early DFTD region and b) mid DFTD region, and devil and mesopredator prey for the c) early DFTD region and d) mid DFTD region. Prefix before .yr represents the appropriate lag time from first year of disease arrival in the region.48*

TABLE 2.2: *Showing the top 3 models and the null model from GLMM analysis of variables important for mesopredator occurrence of a) feral cats and b) eastern quolls from the early and mid DFTD arrival regions. Table shows small sample corrected $\Delta AICc$ and associated weights (w_i), model coefficient estimates with ± 1 SE, σ = standard deviation of random effect. Model explanatory variables identify which species were considered to be important to the species of interest. Rain = current year rainfall deviation, rain.1yr = rainfall deviation lagged by one calendar year. The relative importance of the variable denotes the sum of weights of all candidate models containing the variable, despite not all models being shown. ..51*

TABLE 3.1: *GLMM model outputs testing the assertion that introduced species comprise a greater proportion of the community with increasing time since DFTD arrival. k = model parameters, w_i = weight held by the model within the candidate model set.79*

TABLE 3.2: *Most parsimonious GLMM models and parameter estimates for top order carnivores for hair trap data analysis with $\Delta AICc$, k = parameters, model weight (w_i) and model coefficient estimates with ± 1 SE. Dashed lines highlight the most heavily weighted models from the candidate model set within $\Delta AICc$ of two. Parameter estimates are included for these models only, with X denoting the presence of variables in lower ranked models; not all models are shown. Relative importance of variables represents the weight of all models which contain that variable. Vege type parameters are against coastal scrub, W = Wet mature eucalypt forest, D = Dry eucalypt forest, WR = Wet eucalypt regeneration forest. NA = Not assessed for that species.84*

TABLE 3.3: *Most parsimonious GLMM models and parameter estimates for mesopredator prey species for hair trap data analysis with $\Delta AICc$, k = parameters, model weight (w_i) and model coefficient estimates with ± 1 SE. Dashed lines highlight the most heavily weighted models from the candidate model set within $\Delta AICc$ of two. Parameter estimates are included for these models only, with X denoting the presence of variables in lower ranked models; not all models are shown. Relative importance of variables represents the weight of all models which contain that variable. Vege type parameters are against coastal scrub, W = Wet mature eucalypt forest, D = Dry eucalypt forest, WR = Wet eucalypt regeneration forest.85*

TABLE 3.4: Activity time data available on devils and each mesopredator species by region with the number of detections closest to sunset or sunrise. The data represents the total number of camera videos recorded with repeat animals removed (see Methods). Results of the Fishers Exact tests compare differences in activity between sunrise and sunset among disease regions.	87
TABLE 3.5: GLMM model analysis for the activity times of native mesopredators, the spotted tail quoll and eastern quoll, showing $\Delta AICc$, model weight (w_i) and model coefficient estimates with ± 1 SE. Only the top candidate models which are within $\Delta AICc$ of two are included in the table. Disease region estimates are compared against the disease free region for spotted tail quolls, and the early region for eastern quolls who are not present in the disease free region.	89
TABLE 4.1: The best supported models from the GLM analysis assessing factors affecting the activity index of possums measured through hair-trap hit rates	118
TABLE 4.2: The set of Cox proportional hazards models within a $\Delta AICc$ of 2.0 for the number of nights for a possum to find food patches across a predation risk gradient. The table shows the model rank, the change in $AICc$ ($\Delta AICc$) from the top model, model weights (w_i) and model coefficient estimates ± 1 SE for each explanatory variable. An * indicates $p < 0.05$, ** indicates $p < 0.01$. The relative importance of the variable denotes the sum of weights of all candidate models containing the variable, despite not all models being shown here.	119
TABLE 4.3: Estimated Hazards Ratios and 95% Confidence Interval Estimates for variables in the best supported Cox proportional hazard model of the time until feeding patches were found across the predation risk gradient.	121
TABLE 4.4: Most parsimonious GLMM model with explanatory variables for giving up densities and model parameter estimates explaining the importance of factors in possum anti-predator behaviour. The response variable is the number of sultanas remaining in a feeding patch.	122
TABLE 5.1: Prevalence of IgG antibodies to <i>T. gondii</i> in Tasmanian pademelons. Cat density is the estimated value of the number of cats per transect within the region for data aggregated over 8 years.	145
TABLE 5.2: The most parsimonious GLM models of factors influencing the seroprevalance of <i>T. gondii</i> in pademelons. k = number of model parameters, $\Delta AICc$ represents the difference in $AICc$ from the most parsimonious model, w_i = model weight.	146

Chapter 1: General Introduction



1.1 The ecosystem effects of apex predator loss in a global context

Apex carnivores have been extirpated from the majority of ecological communities worldwide (Terborgh et al. 2001) affecting the integrity and resilience of entire ecosystems (Wallach et al. 2010). The consequences of this loss can represent a significant threat to biodiversity and correspond to increasingly homogenised and invasive-driven ecosystems (Terborgh et al. 1999, Wallach et al. 2010, Estes et al. 2011). The ecological effects of apex predator decline have demonstrated consistent patterns in a broad range of cascading effects through food webs. For example, in areas devoid of an ecologically functional apex predator consequences include species extinctions (e.g. Crooks and Soulé 1999, Johnson et al. 2007), transformation of predator guilds (e.g. Crooks and Soulé 1999, Berger and Gese 2007, Gehrt and Prange 2007), alteration of community composition (e.g. Terborgh et al. 2001, Beschta and Ripple 2009) and behavioural shifts in prey (Fortin et al. 2005, Byrnes et al. 2006). Such ecological effects, observed in a variety of ecosystems on large spatial scales, illustrates the consistent and universal role apex predators play in ecosystem structure and function.

As apex predators are lost from ecosystems worldwide, ecological theory is burgeoning with research into concepts surrounding predator dynamics and ecosystem responses. Trophic cascade theory (Paine 1980) and the mesopredator release hypothesis (MRH) (Soulé et al. 1988) are recent concepts which have gained considerable support from studies in taxonomically and geographically diverse ecosystems following apex predator loss (e.g. Pace et al. 1999, Heithaus et al. 2008, Estes et al. 2011). Both arose following evidence of ecosystem instability and structural change subsequent to the loss of an ecologically functional apex predator. Trophic cascade theory (Paine 1980) describes the process by which the removal of an apex predator has a cascading effect through lower levels of the food web,

increasing herbivore prey abundance and consequently decreasing plant biomass in a series of interconnected links (Paine 1980, Pace et al. 1999, Schmitz et al. 2004). The MRH describes the situation in which smaller predator populations increase when released from exploitative and interference competition from their larger counterparts (Soulé et al. 1988) which in turn can induce cascades down the food web by influencing populations of their prey species.

Since their inception, the collective evidence in support of these hypotheses has been substantial from studies arising from both “natural experiments” (e.g. Rogers and Caro 1998, Crooks and Soulé 1999, Terborgh et al. 2001) or retrospectively with the re-introduction of large predators (e.g. Ripple and Beschta 2007, Berger and Conner 2008).

Evidence of trophic cascades has been demonstrated in all major biomes on earth (Estes et al. 2011) and has also been supported by a large number of studies. The notion of a trophic cascade was classically considered to occur along linear food chains from predator to consumer to plant communities (Paine 1980), however, more recently it has been more broadly defined in terms of any cascade in food web ecology incorporating more than one link in the food web (Pace et al. 1999). The disruption of predator-prey relationships can induce trophic cascades through changes in prey dynamics and behaviour (Berger 1999, Pace et al. 1999, Schmitz et al. 2004). Perhaps one of the most renowned examples of terrestrial trophic cascades occurred in the Yellowstone ecosystem in the United States. The extirpation of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) more than half a century ago, translated into greater herbivore juvenile survivorship and increased grazing pressure, resulting in structural changes in vegetation communities (Beschta and Ripple 2009) and a concomitant decline in avian fauna diversity (Berger et al. 2001). Reintroductions of wolves in the mid-1990's resulted in increased vigilance of both bison (*Bison bison*) and elk (*Alces alces*)

(Laundre et al. 2001) and a change in preference of elk for particular habitat types with a lower risk of wolf encounters (Fortin et al. 2005).

Evidence for mesopredator release has been demonstrated on every major landmass except Antarctica (Prugh et al. 2009). In a review of the mesopredator release literature, an overwhelming 95% of studies found at least some evidence to endorse it (Ritchie and Johnson 2009), although the potential for a publication bias cannot be ignored (Brashares et al. 2010). There is convincing evidence that the largest extant predator in Australia, the dingo (*Canis lupus dingo*), protects smaller native marsupials from decline and extinction through the suppression of invasive red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) (Smith and Quin 1996, Glen and Dickman 2005, Johnson et al. 2007, Letnic et al. 2009b). The dingo is subject to severe persecution, particularly in areas of livestock grazing (Johnson et al. 2007) and it is now absent from many parts of the continent (Fleming et al. 2001). Globally, mesopredators are becoming the dominant force in driving community dynamics. Both introduced and native species formerly considered mesopredators are now filling apex predator niches and defining new ecosystem states (Roemer et al. 2009).

Where apex predators have been functionally extirpated, mesopredators may fulfil a surrogate role (Terborgh et al. 1999) and though they are not ecologically equivalent (Prugh et al. 2009), they may be the driving force behind community structures (Roemer et al. 2009).

Mesopredators, which are often more abundant than their larger apex counterparts, have greater species diversity and offer more variety in both behaviour and ecology (Roemer et al. 2009), are one of the key guild levels to benefit from apex predator loss. An example from North America highlights the complexities of apex and mesopredator relationships. Here, the success of ground nesting birds is positively associated with higher populations of the most

common apex predator, the coyote (*Canis latrans*), which suppresses the major predators of these birds, racoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) (Rogers and Caro 1998, Crooks and Soulé 1999, Gehrt and Prange 2007). The coyote itself has undergone mesopredator release with the extirpation of gray wolves (*Canis lupus*) from much of its range by the 1930's (Berger and Gese 2007), with some retrospective evidence of effects on pronghorn (*Antilocapra americana*) fawn survival (Berger and Conner 2008, Berger et al. 2008). In this way the coyote, historically a mesopredator, is now an apex predator, though it still exhibits mesopredator traits such as a diverse and opportunistic diet and ability to maintain large populations despite continual persecution (Terborgh et al. 1999, Prugh et al. 2009, Roemer et al. 2009). This situation may be common in complex multi levelled carnivore guilds in which the former apex predator has been functionally extirpated (Roemer et al. 2009).

The extent to which top-down and bottom-up forces influence biodiversity within an ecosystem remains contentious (Terborgh et al. 1999, Estes et al. 2011). Bottom-up effects, which incorporate food availability and habitat structure, need to be considered in addition to top-down processes to ensure that the key factors which drive ecosystem changes and influence their magnitude are accurately identified (Ritchie and Johnson 2009). The likelihood of occurrence of mesopredator release and its magnitude is determined by the productivity of the ecosystems and the strength of the relationships between apex predators, mesopredators and prey (Brashares et al. 2010). Elmhagen and Rushton (2007) were the first to demonstrate top-down and bottom-up effects acting concurrently on mesopredator populations with a large spatial study across different bioclimatic regions in Sweden. Here, there was evidence of mesopredator release of red foxes subsequent to the decline in wolves and lynx (*Lynx lynx*).

Ecosystem productivity, however, determined its magnitude with highest productivity regions demonstrating the strongest mesopredator response (Elmhagen and Rushton 2007). Increases in mesopredator abundance have also been attributed to urbanisation as demonstrated in raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) in North America, as a result of artificially induced bottom-up control, where they can effectively exploit anthropogenic food resources (Prange and Gehrt 2004). For taxonomically diverse herbivore species, rainfall and resource availability are a major influence on juvenile survivorship and reproductive potential (e.g. Fisher et al. 2001, Owen-Smith et al. 2005), which can have corresponding effects on populations of their predators. Bottom-up processes can play a key role in driving ecosystem structure and influencing biodiversity and such effects which may confound or restrict the effects of apex predator loss should be considered in ecological studies.

1.2 The vulnerability of large mammals and apex predators in particular to extinction

Many species which still persist in the wild represent only a fraction of their historical population levels and occupy only remnants of their former distributions (Morris et al. 2009). Human population expansion and its associated effects, including habitat degradation, persecution and introduction of invasive species, are fundamental components in almost all recent and continuing species declines and extinctions (Cardillo et al. 2004). In particular, evidence suggests that larger bodied species at higher trophic levels have environmental, ecological and intrinsic biological traits that place them at a greater risk of extinction than their smaller bodied counterparts (Purvis et al. 2000, Purvis et al. 2001, Duffy 2003, Cardillo et al. 2005). The body weights of mammalian species which are threatened with extinction are

on average an order of magnitude higher than species which are non-threatened and with continuing environmental and anthropogenic pressures, the declines of larger bodied species will be more rapid than smaller bodied species with similar biological traits (Cardillo et al. 2005). Factors shown to affect the positive association of extinction risk and body mass include human population density, species geographic range and population density, number of litters per year and gestation length (Cardillo et al. 2005). Multiple combinations of these factors may have a cumulative effect with increasing body size (Cardillo et al. 2005). High trophic level, also correlated with extinction risk (Duffy 2003), demonstrates the importance of interacting components in the food web to species resilience. So, while a species might not demonstrate characteristics which place them at increased risk of extinction, they may depend on species which do exhibit such traits (Purvis et al. 2000).

The biological characteristics of a species determine how well it can respond to threats (Cardillo et al. 2004, Purvis et al. 2005). There are many intrinsic factors that are thought to increase the extinction risk of species including small population sizes, low population densities, slow life histories traits including long gestation times and small litter sizes, complex social structures, a small geographic range and a large home range (Purvis et al. 2000, Gittleman et al. 2001, Cardillo et al. 2005). Large carnivores epitomise many of these intrinsic characteristics (Gittleman et al. 2001). It has been demonstrated that small population size, exacerbated by a slow life history, increases the risk of extinction when external threats are high (Cardillo et al. 2004). An environmental perturbation may disrupt population sizes and demographic processes may lead a population to local or global extinction. Hence, biological characteristics inherent in large carnivores combined with the magnitude and scale of anthropogenic pressures from habitat destruction, fragmentation, pollution, bio-

accumulation of toxins, persecution and domestic pathogen exposure faced by large carnivores make them particularly susceptible to local and global extinction (Purvis et al. 2000, Cardillo et al. 2005, Estes et al. 2011) This is reflected in the corresponding demise of large mammalian predator populations from the majority of terrestrial ecosystems worldwide (Terborgh et al. 2001, Estes et al. 2011).

1.3 Disease in wildlife and apex carnivores

The number of emerging infectious diseases reported in wildlife is increasing, and while this can in part be attributed to increased levels of vigilance and monitoring, the evidence for increasing prevalence of infectious disease appears to be compelling in the face of environmental degradation and worldwide homogenization of ecosystems (Daszak et al. 2000, Dobson and Foufopoulos 2001). Increased exposure to feral and domestic animals (e.g. Thorne and Williams 1988, Dobson and Foufopoulos 2001), and biodiversity loss (Keesing et al. 2010) are two examples which have both been associated with increased disease risks, by affecting host or vector ecology, and have played a primary role in many recent emerging diseases with significant population declines (Schrag and Wiener 1995). Wildlife cancers too are gaining increasing recognition as indicators of environmental disturbance from anthropogenic effects and are now considered an important cause of mortality in several species (McAloose and Newton 2009). Widespread loss of genetic diversity could see the emergence of directly transmissible cancers, a new type of natural enemy (McCallum and Jones 2012).

Extensive population declines at top trophic levels have been associated with recent infectious disease outbreaks. Examples include canine distemper in lions (Kissui and Packer 2004) and

black footed ferrets (Thorne and Williams 1988), a transmissible cancer in Tasmanian devils (McCallum et al. 2007) and Ebola in African apes (Leroy et al. 2004). Not only have such population crashes underscored the importance of disease threats to individual species of conservation concern, they have highlighted our lack of understanding of the role that diseases play in population regulation and the ensuing disruption of ecological structure and function. Population and community-level effects of wildlife disease are relatively poorly understood due to inherent difficulties of monitoring and sampling wild animal populations for the detection and diagnosis of disease (Scott 1988, Thompson et al. 2010).

Disease induced population declines in wild mammals are not consistent across trophic classes. In herbivores, the majority of population declines are attributed to starvation, but contrastingly for carnivores it is linked with disease (Young 1994). This may be because carnivores, and in particular apex predators, are at a disproportionate risk from anthropogenic factors that may increase the risk of being exposed to infectious diseases as well as possessing life history characteristics that render them vulnerable to population decline. Anthropogenic factors are found to be responsible for assisting pathogen infection in over half of disease outbreaks observed (Dobson and Foufopoulos 2001). Carnivores as a general group tend to have larger home ranges and longer life spans which mean they come into contact with human development and a large array of environmental contaminants throughout their life, including exposure to domestic animals and bio-toxins (Funk et al. 2001). Both their diet and more complex social structures may also facilitate disease transmission (Young 1994, Funk et al. 2001). Disease risk may be further confounded by reduced genetic variability which can affect the ability to respond immunologically to new disease challenges and is associated with small population sizes, bottlenecks and habitat fragmentation of some carnivore populations

(Funk et al. 2001). This is evident in the emergence of both naturally occurring transmissible cancers in carnivores, the Canine Transmissible Venereal Sarcoma (CTVS) and the Tasmanian devil facial tumour disease (DFTD), which are both thought to have evolved in genetically restricted populations (Murgia et al. 2006, McCallum 2008, Murchison 2008). Diseases may exert top down regulatory control on apex predator populations which, by the very nature of their trophic position and life history characteristics, are more vulnerable to emerging infectious diseases, at least in the short-term, influencing entire ecological communities and food webs.

1.4 The Tasmanian Devil and DFTD

Tasmanian devils (*Sarcophilus harrisii*), the largest extant marsupial carnivore in the world and endemic to Australia's island state of Tasmania, are currently facing the real possibility of disease-induced extinction in the wild due to a consistently fatal transmissible cancer (Hawkins et al. 2006, Lachish et al. 2007, McCallum et al. 2009). The disease has been aptly termed devil facial tumour disease (DFTD) after the large gross lesions forming mostly around the face and neck (Figure 1.1). To date the disease has resulted in population declines of devils of more than 80% across the island of Tasmania with long-term diseased sites demonstrating more than 95% reduction in pre-diseased populations (Save the Tasmanian Devil Program 2012). The disease, first discovered in the far north-east of Tasmania at Mt William National Park in 1996, now covers more than 75% of the devils current geographic range and is continuing to spread (Save the Tasmanian Devil Program 2012) (Figure 1.2). This has led to the listing of devils as 'Endangered' at state (*Threatened Species Protection Act 1995*), federal (*Environment Protection and Biodiversity Conservation Act 1999*) and

international (IUCN Red List 2012) levels. Devils still persist in low densities in long-term disease regions, though so far there has been no evidence of population recovery. In the absence of any significant developments in reducing the threat of DFTD to wild devil populations, the population of devils will continue to decline over much of Tasmania in the immediate future and remain at significantly depressed levels for decades.

DFTD is spread by allograft in which infectious cells are essentially transplanted into an uninfected animal by biting (Pearse and Swift 2006), which frequently occurs when animals fight over carcasses and during the mating season (Hamede et al. 2009). This type of infectious cancer cell line is extremely rare and has only been observed in one other instance in wild free-ranging species; Canine venereal transmissible sarcoma (CVTS), a sexually transmitted disease in dogs (Das and Das 2000, McCallum 2008). The latent period of the disease is currently unknown, however once devils show clinical signs, very few survive for more than six months (Beeton and McCallum 2011). Devils have low levels of genetic diversity relative to other Australian marsupial carnivores (Jones et al. 2004a) which may have contributed to the evolution of DFTD.



FIGURE 1.1: *Two separate devils infected with DFTD, both in an advanced stage. DFTD is named after the gross lesions which often form around the face and neck.*

Transmission of DFTD is frequency dependent, meaning the disease is spread in the same manner as a sexually transmitted disease, maintaining a high force of infection even at low population densities (Hamede et al. 2008, McCallum et al. 2009). This type of disease transmission can lead to extinction of infected populations (de Castro and Bolker 2005) and is likely the reason why attempts to control DFTD through selective culling have been unsuccessful (Lachish et al. 2010, Beeton and McCallum 2011). The spread of DFTD has not been consistent across the landscape. The disease spread 270km south in the 11 years following its initial discovery in 1996 and 190km west-southwest during the same period, the disparity likely arising from differences in movement patterns through variable habitats (McCallum et al. 2007).

Devils and thylacines (*Thylacinus cynocephalus*), a larger apex marsupial predator, were historically distributed across the majority of mainland Australia. Both became extinct following the introduction of the dingo (Corbett 1995) and the escalation of threats from increasingly sedentary humans (Johnson and Wroe 2003) between 3000-4000 years ago (Brown 2006), though the exact cause of their mainland extinction and timing of the extinction remains controversial. When European settlers arrived, both the devil and the thylacine were found only in Tasmania. Following European settlement both devils and the thylacine suffered extreme persecution from bounty schemes. Thylacines went extinct in the 20th century, with the last individual officially recorded in 1936 (Guiler 1985). Devils were subsequently provided with legal protection in 1941 but had already suffered widespread and severe declines. Secondary poisoning from strychnine may also have had a heavy toll on devil populations until it was phased out as a rabbit control method in the early 1950's (Hawkins et al. 2006). Devil populations recovered and the pre-DFTD population has been estimated at

approximately 60,000 individuals (Beeton 2012). Since the extinction of the thylacine in Tasmania, devils have been the dominant predator, potentially taking on the role of surrogate apex predator, though they are ecologically and morphologically very different.

Tasmanian devils are specialised scavengers with a diverse diet (Owen and Pemberton 2005), however, they are also effective pounce pursuit predators with a preference to hunt in open habitats (Jones and Stoddart 1998). Their diet is predominantly comprised of larger-bodied native species including the brushtail possum (*Trichosurus vulpecula*) and Tasmanian pademelon (*Thylogale billardierii*), although they will consume a wide range of small- and medium-sized mammals, birds and invertebrates (Jones and Barmuta 2000). Devils have adaptations for scavenging which include strong teeth and skull allowing them to consume all parts of a carcass including bone (Jones 2003). Biomechanical analyses suggest that they can exert the strongest bite force relative to body size of any living mammal (Wroe et al. 2005). Devils are nocturnal, largely solitary and not territorial, with large home-ranges averaging 13km² (Pemberton 1990). Prior to DFTD arrival they were widespread and have been recorded in all Tasmanian vegetation types (Rounsevell et al. 1991), though highest densities are found in dry sclerophyll forest and coastal scrub. Devils are sexually dimorphic with males (~11kg) being larger than females (~7kg) and they can live for up to 6 years in the wild (Pemberton 1990, Jones 1997). Devils breed once a year from age two and have a very defined breeding season beginning in early March, with a gestation period of approximately three weeks (Pemberton 1990, Hesterman et al. 2008). They give birth to as many as 30 live young but can only rear a maximum of four because they have only four teats in their pouch.

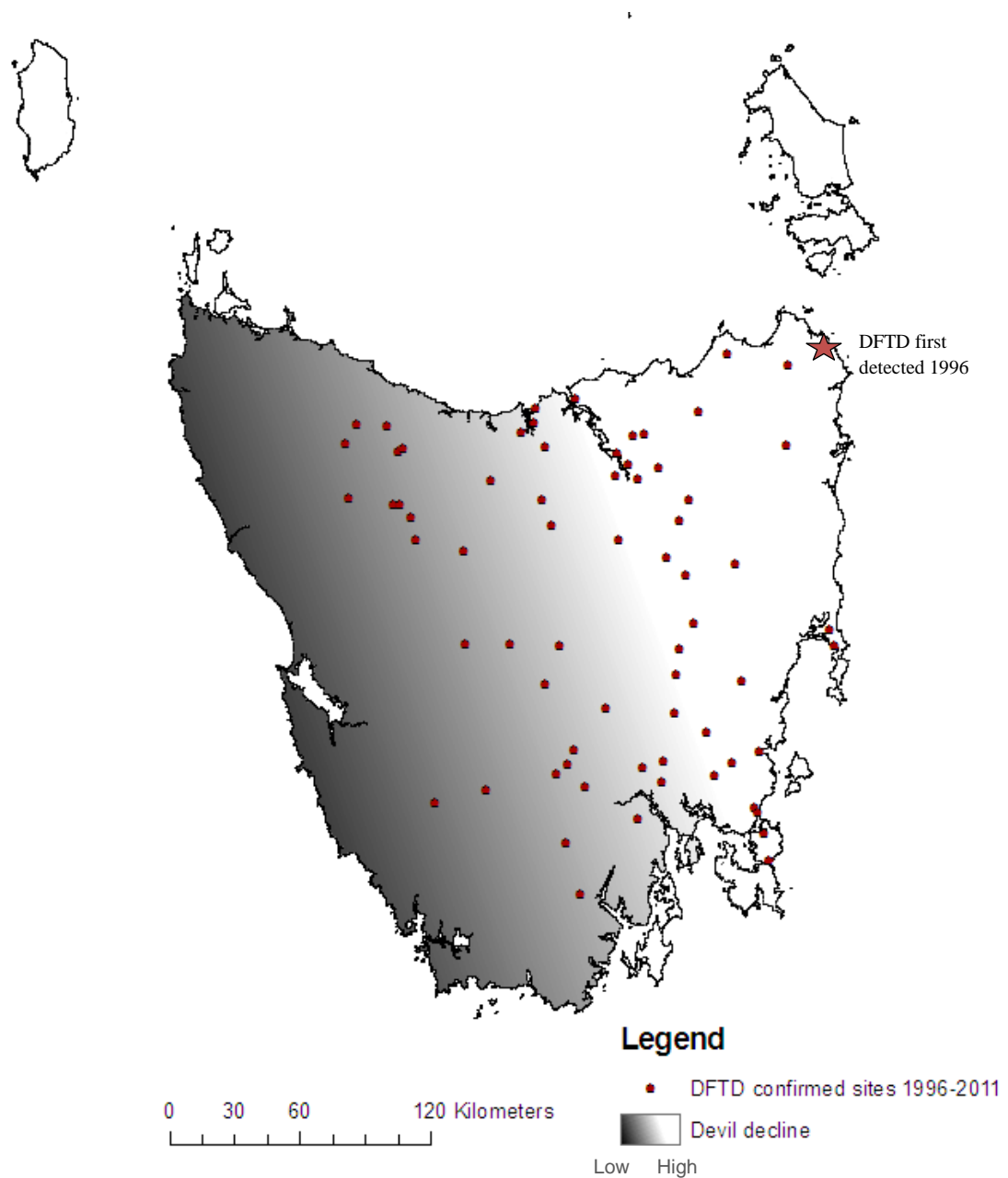


FIGURE 1.2: Map of sites where DFTD has been confirmed prior to 2012. Devil decline is highest in areas of long-term disease in the eastern part of the state. Devils are not present on offshore islands. (Data from Department of Primary Industries, Parks, Water and Environment; Hawkins *et al*, 2006).

1.5 The Tasmanian ecosystem

The Tasmanian devil may currently be the largest extant terrestrial carnivore in Tasmania, but it was a mid-sized mesopredator in the historical Tasmanian ecosystem. Devils still possess many intrinsic biological traits that are common to mesocarnivores, including being highly abundant prior to DFTD despite persecution, opportunistic feeders, living in a diverse array of habitats and potentially being a major force in driving community structure. Unfortunately there is no published evidence for ecosystem effects directly related to the eradication of the thylacine, making inferences about the devil's role in community structures prior to thylacine extinction difficult.

Despite the extinction of the thylacine, Tasmania retains the most complex multi-level carnivore guild in Australia, with higher orders comprising the Tasmanian devil, the native marsupial spotted-tailed quoll (*Dasyurus maculatus*) and the introduced placental cat, as ecologically similar mesopredators, and the eastern quoll (*Dasyurus viverrinus*) as a smaller native marsupial mesopredator. In addition, there are low but breeding populations of the recently introduced red fox (Saunders et al. 2006, Sarre et al. 2012), the ecological effects of which are uncertain. In terms of competitive interactions, there is evidence of current and long-term interspecific and aggressive interference competition between the three native species within the higher order carnivore guild, which has led to competitive character displacement in the trophic structures (Jones 1997, Jones 1998, Jones and Barmuta 1998). Within the guild, the spotted-tailed quoll would be expected to experience the most extensive competition as it overlaps in diet with both the larger devil and the smaller eastern quoll (Jones and Barmuta 1998). In addition, the introduced feral cat would likely compete with the spotted-tailed quoll due to its similar size and prey range (Dickman 1996, Glen et al. 2011).

Being the smallest carnivore in the guild, eastern quolls are at greatest risk of aggressive interference competition and predation from all species, but particularly from the larger spotted-tailed quolls and feral cats (Jones et al. 2004b). Feral cats are known to predate on the similar sized northern quoll (*Dasyurus hallucatus*) on mainland Australia (Oakwood 2000). Eastern quolls have been extirpated from mainland Australia, and predation from larger introduced predators, particularly the red fox, has been implicated in its demise (Jones et al. 2003). This, along with a lack of anti-predator response to introduced carnivores, highlights the eastern quolls vulnerability to any increase in predation threats (Jones et al. 2004b).

Nearly 50% of all mammal extinctions worldwide over the past two centuries have occurred in Australia (Short and Smith 1994) and the majority of these extinctions have occurred in the prey size range of introduced mesopredators. Of placental native rodents, 19% are now extinct compared with 6% of the total mammalian fauna (Smith and Quin 1996). Feral cat abundance was the biggest predictor in the declines of the smallest of these species and where dingoes were present, declines were less severe (Smith and Quin 1996). Tasmania remains the last refuge for species extinct or critically endangered on mainland Australia including the eastern quoll, the Tasmanian bettong (*Bettongia gaimardii*), the Tasmanian pademelon (*Thylogale billardierii*) and eastern barred bandicoot (*Perameles gunnii*) (Recher and Lim 1990). The disappearance of these and other similar sized native species from the Australian mainland has been attributed to introduced predators, the red fox and feral cat (Short and Smith 1994, Glen and Dickman 2005). Any increase in introduced and native mesopredators, thought to be largely controlled through competitive suppression from Tasmanian devils, could potentially devastate native Tasmanian fauna, the majority of which fall within the prey size range of larger mesopredators.

There have been several reported historical and largely accidental incursions of the red fox into Tasmania but it was considered fox free up until 1999 when there is substantial evidence that foxes were systematically and illegally introduced between 1999 and 2001 (Saunders et al. 2006). There is now evidence of a small but breeding population of foxes in Tasmania (Sarre et al. 2012). As co-occurrence of devils and foxes is novel, the interaction between these two species, including potential mesopredator suppression of foxes by devils, is unknown. Foxes may have previously been limited by devils, in the same way that dingoes appear to have limited fox populations. To date, there is no evidence for ecological impacts of the red fox in Tasmania due to its recent arrival and very low population estimates, which are largely inferred from broad-scale scat collections. Because of their low population size, foxes have not been studied as part of this thesis and are not discussed in extensive detail hereafter.

The common brushtail possum, the Tasmanian pademelon and the larger Bennett's wallaby (*Macropus rufogriseus*) are the largest and most dominant native herbivores in the Tasmanian ecosystem (the Forester kangaroo *Macropus giganteus* is considerably larger but is not widespread and abundant). All three species are subject to regular culling in the hundreds of thousands annually under crop and pasture protection permits (Tasmanian State Planning Commission 2009). Additionally the common brushtail possum is harvested for the minor fur industry.

Tasmania has a complex ground-dwelling small mammal community, comprising three native carnivorous marsupials, five species of native rodent and an additional three introduced rodents, which are widespread: the house mouse (*Mus musculus*), the black rat (*Rattus rattus*) and the brown rat (*Rattus norvegicus*). The black rat has been shown to be competitively dominant over some native rodent populations on mainland Australia (Stokes et al. 2009), but

little is known about the interactions in Tasmanian small mammal fauna or on endemic Tasmanian species.

Tasmania has a temperate environment, with environmental gradients across the state that influence the geographic distribution of some species. Rainfall generally increases from east to west, and a temperature gradient runs from north to south. The vegetation of Tasmania (see Harris and Kitchener 2005) is predominantly dry sclerophyll forest, woodland and native grassland in the north-east with large tracts of wet eucalypt forest in the mountainous regions near Ben Lomond. In the north-west the vegetation is much more diverse, with large areas of tussock moorland, wet scrub, rainforest and wet eucalypt forest, which is indicative of the significantly higher rainfall. Mid regions of the state are dominated by cleared agricultural lands and dry sclerophyll forest and woodland. These regional variations explain geographic limitations in the distributions of some species with specific habitat requirements. For example, the Tasmanian bettong, which is abundant in dry sclerophyll forest but it has not been recorded anywhere in the entire western part of the state (Rounsevell et al. 1991). The eastern quoll is also extremely rare or absent in the north-west, with populations predominantly in the drier open forests and grasslands of the east (Rounsevell et al. 1991, Jones and Rose 1996)

1.6 Predictions for Tasmania based on lessons learned globally

Fundamental theories in community ecology with broad and repeated consensus within the international literature can be used to predict some of the likely ecosystem effects of apex predator decline in the Tasmanian context. Trophic cascade theory predicts a raft of cascading effects through increasingly lower levels of the food web (Paine 1980, Pace et al. 1999). The

absence or reduction of apex predators has been shown to influence levels of the food web far removed from the apex predator themselves including invertebrate (Terborgh et al. 2001) and vegetation communities (Beschta and Ripple 2009, Letnic et al. 2009b). In Tasmania, reduced biodiversity and ecosystems dominated by invasive species may become common, following the loss of two apex predators in less than a century.

In the Tasmanian environment, it is predicted that the feral cat and native spotted-tailed quoll would increase in abundance and reduce their avoidance behaviours when released from exploitative and interference competition, as predicted by the mesopredator release hypothesis (Soulé et al. 1988). Any evidence of mesopredator release in larger mesopredators may result in a concomitant decline in eastern quolls, which may previously have been indirectly protected by their suppression. Other native fauna species within the prey range of spotted-tailed quolls and feral cats, largely small and medium-sized mammals and avian fauna (Belcher 1995, Dickman 1996), may decrease, including those which are extinct or critically endangered on mainland Australia, such as the Tasmanian bettong and eastern barred bandicoot (Recher and Lim 1990). For small mammals, competitively dominant introduced species, such as the black rat, may begin to dominate over native species in areas with increased predation pressure from larger mesopredators. This could occur if increased predation pressure differentially affects native rodents and through potential naïveté to introduced predators: the native swamp rat (*Rattus lutreolus*) has been shown to be unresponsive to cat scent (McEvoy et al. 2008). Birds, which are frequently found in the diet of both species, may be at an increased risk due the partially arboreal nature of both spotted-tailed quolls and cats (Belcher 1995, Dickman 1996). There is also a real risk of red fox populations becoming established in Tasmania.

The extensive environmental gradients across Tasmania, suggest that there may be variation in the magnitude of top-down control on the ecosystem. Productivity has been shown to influence the degree of mesopredator release in other ecosystems (Elmhagen and Rushton 2007). Variables such as rainfall and temperature which are not consistent across the state, could affect the relative productivity of different regions. Therefore in some ecosystems in Tasmania it could be expected that the top-down force exerted by devils may be dampened, and bottom-up forces of prey and habitat availability may play a greater role in influencing mesopredator populations. These ecosystems may be defined by lower productivity, including lower rainfall.

Key species in the diet of devils, such as Tasmanian pademelons and common brushtail possums (Jones and Barmuta 1998), may increase in abundance and reduce their anti-predator behaviours. Any of these changes could lead to increased grazing pressure and changes to vegetation structures which have been observed both on mainland Australia (Letnic et al. 2009b) and elsewhere (Terborgh et al. 2001, Beschta and Ripple 2009) following the release of the prey species of apex predators. This may lead to complex effects on tree recruitment, soil composition, forest age structures, vegetation species composition and invertebrate communities. At these levels of the food web the culmination of external factors has a multiplying effect through proceeding links in the food web and attributing the magnitude of effect of apex predator decline can be problematic.

For devil prey species, there may also be an increase in the prevalence of diseases as devils no longer take sick and injured individuals from the populations, with unknown effects on demographic processes. Any increase in transmission agents could increase disease risk. For example, the only known definitive hosts for the parasite *Toxoplasma gondii* are members of

the felid family, but all mammals can act as intermediate hosts. There is the potential for increased prevalence in native wildlife if feral cat densities increase. Species at higher levels of the food web may have higher risk due to multiple routes of infection. Subclinical infection in native species could increase their susceptibility to predation, with behavioural changes to increase transmission rates observed in rats (Webster 1994, Berdoy et al. 2000, Webster 2001) and in so-called dead-end infections of humans (Havlicek et al. 2001, Torrey and Yolken 2003)

Scavenger species such as wasps and ravens may increase due to a higher proportion of carrion in the environment that is no longer being scavenged by devils. Birds such as the masked owl and wedge-tail eagle may increase, but there is little known about the effects of apex terrestrial predator decline on avian predator fauna.

1.7 Thesis context and aims

Determining what constitutes a normal, healthy ecosystem is one of the many great challenges for research endeavours attempting to answer questions on food web ecology and trophic cascade theory. It is imperative to establish ecological indicators which reflect and respond to changes in the health of communities, which are easily measured and provide predictions for the future (Morris et al. 2009). The decline of the Tasmanian devil from DFTD is dramatic and devastating; however it does provide a unique opportunity to assess the ecosystem effects of the loss of an apex predator in a large scale “natural experiment”. Devil decline is drastic and widespread within just a few years of DFTD arrival into a local population, allowing a detailed and comprehensive comparative study across a range of DFTD arrival times.

As the first study to examine ecosystem responses to Tasmanian devil decline, this thesis attempts to provide an overarching foundation for our understanding of the effects associated with apex predator loss in Tasmania. Unfortunately there is no knowledge of the historical effects on faunal communities in Tasmania from the extinction of the thylacine. With the continuing rapid spread of DFTD across the state, this study may provide the only opportunity to comprehensively study ecosystem effects with disease free regions still remaining. As a result the themes are intentionally broad and general in scope with a focus on assessing large-scale facets of the ecosystem which, if disrupted, are expected to have the most significant effect for native species persistence and long-term ecosystem resilience. Results of this study could provide the basis of information to establish minimum management interventions required to maintain ecosystem integrity in the absence of an ecologically functioning devil population. These could be implemented to ensure the long-term population viability of native species and the success of any potential future re-introduction of devils into the wild. Conservation based decisions should reflect the needs of ecosystems and communities rather than a single species (Morris et al. 2009). This project is of paramount importance to determining some of the conservation needs of Tasmania's ecosystems and defining conservation strategies that will be effective for the entire community and not just the devil.

Apex predator decline and mesopredator release studies rarely take into account bottom-up effects and environmental variables in large scale systems. The presence of environmental gradients across Tasmania adds an extra level of complexity and may confound issues of apex predator decline without careful consideration, but it also provides a unique opportunity to assess productivity and its effects on top-down and bottom-up regulation.

This thesis endeavours to provide insights into the extent and magnitude of ecosystem disruption associated with apex predator decline in Tasmania, and aims to determine common themes which may apply globally. This includes analysis of whether Tasmania's ecosystem is moving to a more invasive and pest driven state from which recovery would be exceedingly difficult, as well as gauging the value of accounting for environmental productivity when assessing top-down control. The specific concepts assessed in this study relate to changes in abundance, activity and behaviour, and disease risk of both native and invasive species.

Primary aims of this study were to assess broad-scale effects of Tasmanian devil decline on (1) the relative abundance and activity levels of a wide range on native and introduced species with particular consideration given to mesopredators, including the influence of productivity on the magnitude of top-down and bottom-up control of mesopredator populations; (2) changes to species compositions including the likelihood of increasingly invasive and homogenised community states (3) behavioural implications of mesopredators and devil prey species in response to declining devil populations; and (4) the disease risk for native species following an increase in introduced mesopredator populations.

1.8 Thesis structure

The thesis is structured into three distinct areas of research assessing the ecosystem effects of DFTD across different levels of the food web; relative abundance, behaviour and disease risk (Figure 1.3). The relative abundance and activity changes of a wide range of introduced and native species across extensive temporal and spatial scales is assessed in chapters two and three. The scope and methodology of these two chapters is very different. The first utilises a long-term state-wide spotlighting dataset (sourced from the Tasmanian state government

conservation agency), and was used to assess the changes in relative abundance of mesopredator and devil prey species before and after the arrival of DFTD into a region. It also evaluates the role of top-down and bottom-up forces in controlling mesopredators across a varied environmental gradient. It was the only data that could be used for the eastern quoll whose geographic range is limited to only diseased regions. This chapter was limited to large bodied species which could be detected when spotlighting from a vehicle and was not appropriate for cryptic carnivores such as the spotted-tailed quoll and small bodied mammals at the lower end of the prey range of mesopredators. Chapter three, the second part in assessing relative abundance and activity, utilised remote motion activated cameras and hair traps deployed at field sites across the northern half of the state in an extensive snapshot survey of animal activity and relative abundance across the entire spectrum of DFTD arrival times. These field methods were designed to assess both community composition and population index measures of mesopredators and the small mammal prey species of mesopredators to assess trophic cascade theory and trace the flow-on effects from apex predator loss through the food web. Behavioural changes are important in assessing any ecosystem consequences of the loss of apex predators so activity times were also assessed for the largest mesopredators who are generally considered to be crepuscular, in response to local abundance of generally nocturnal devils.

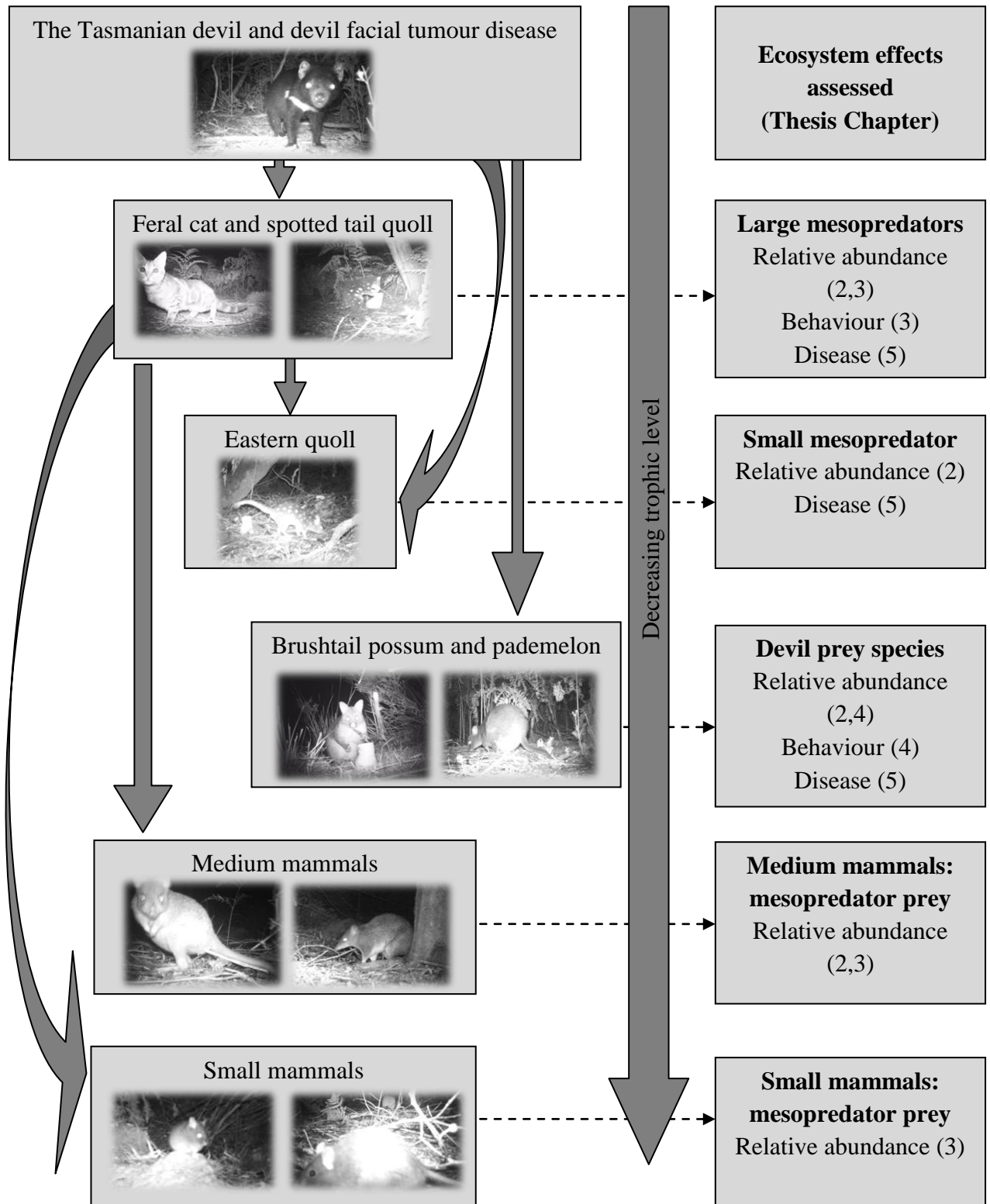


FIGURE 1.3: Thesis structure outlining the questions addressed for species at each trophic level. Arrows represent the species relationships assessed and direction of those relationships

For devil prey species, behavioural changes may also be important in ecosystem stability.

Chapter four assesses a population index measure and a range of anti-predator behaviours of a common devil prey species in response to DFTD arrival. The fifth chapter evaluates the risk of disease transmission to native wildlife in the context of changing mesopredator populations with specific reference to *Toxoplasma gondii* and populations of the definitive host, *Felis catus*. This represents the first time to my knowledge that disease as a consequence of apex predator decline has been evaluated. This is beyond the generally common and apparent assessments of ecosystem consequences of apex predator loss to highlight other potential implications for species with changing ecosystem dynamics and just how extensive those effects may be.

Finally, the concluding chapter discusses the overall implications of Tasmanian devil decline and what support for foundation principals and ecological theories have been uncovered.

Lastly, I propose future directions for apex predator studies and discuss the capacity for ecological restoration to play a role in re-establishing some element of top-down control and ecological resilience.

This chapter has been removed for
copyright or proprietary reasons.

CHAPTER 2

Trophic cascades following the disease-induced decline of an apex predator

Published In:

http://scienceindex.com/stories/3430653/Trophic_Cascades_Following_the_DiseaseInduced_Decline_of_an_Apex_Predator_the_Tasmanian_Devil.html

Hollings, T., Jones, M., Mooney, N., McCallum, H. 2013. Trophic cascades following the disease-induced decline of an apex predator. *Conservation Biology*- DOI: 10.1111/cobi.12152. Article first published online: 11 SEP 2013.

Chapter 3: Disease- induced decline of an apex predator drives invasive-dominated states and threatens biodiversity



3.1 ABSTRACT

Apex predators play an important functional role in protecting and preserving biodiversity. The extensive, worldwide decline in large predator species has been linked with species extinctions, mesopredator release of smaller carnivores and increasingly invasive community states. The Tasmanian devil (*Sarcophilus harrisii*) is the largest extant marsupial carnivore and is threatened with extinction in the wild from a transmissible cancer, devil facial tumour disease (DFTD). The disease has been responsible for population declines in excess of 95% in long-term diseased areas and has spread to more than 75% of the devil's current range. I conducted a rapid snapshot survey across a large spatial extent to assess the response of terrestrial mammalian fauna to devil decline through relative measures of community composition, population indexes and activity times. The results provide evidence that the devil plays a keystone role in Tasmania's ecosystem and their decline is negatively impacting on biodiversity. In areas of long-term devil decline species composition was more homogenous and invasive species comprised a significantly larger proportion of the community. Invasive species at all trophic levels responded positively to devil decline. In contrast, native counterparts showed decreasing trends or no significant response. There was support for mesopredator release in the invasive feral cat, but not in the native spotted-tailed quoll which is of comparable size and has a similar prey composition. Small native mesopredator prey species exhibited significantly smaller population index measures with increasing years since DFTD arrival, which represents a proxy for devil population decline over time. In contrast, introduced rodents were positively associated with larger mesopredator populations. Eastern quolls, the smallest of the native mesopredators, exhibited significantly different activity times in relation to varied devil abundance; however limited geographic range precluded further

analysis for this species. This study provides evidence for ecosystem changes in areas of apex predator loss which have the potential to affect the long-term persistence of native species.

3.2 KEY WORDS

Tasmanian devil; mesopredator release; DFTD; apex predator; Tasmania; invasive species; camera surveys; hair traps; feral cat

3.3 INTRODUCTION

Severe and unprecedented declines of apex predators are occurring in ecosystems worldwide (Pace et al. 1999, Dalerum et al. 2009, Prugh et al. 2009). This is a result of their vulnerability to a multitude of increasing environmental and anthropogenic stressors, including habitat fragmentation, emerging diseases and persecution. Evidence suggests that the loss of apex predators is playing a considerable role in the transition to more homogenised (Estes et al. 2011) and invasive (Wallach et al. 2010) ecosystem states. Apex predator decline has been linked to changes in community composition (Terborgh et al. 2001), extinction of species at lower trophic levels (Crooks and Soulé 1999, Johnson et al. 2007) and behavioural changes in both mesopredator (Creel and Creel 1996, Durant 2000) and prey species (Ripple and Beschta 2003).

Where apex predators have been functionally extirpated, mesopredators may fulfil a surrogate role and though they are not ecologically equivalent (Prugh et al. 2009), they may become the driving force behind community structures (Roemer et al. 2009). Mesopredators, which are often more abundant than larger apex predators, have greater species diversity and offer more variety in both behaviour and ecology (Roemer et al. 2009) are one of the key guild levels to benefit from apex predator loss (Ritchie and Johnson 2009). Mesopredator release occurs when the abundance of smaller carnivores increases after being released from competitive and exploitative competition from larger competitors (Soulé et al. 1988). Evidence for mesopredator release has been demonstrated on every major landmass except Antarctica (Prugh et al. 2009). The prey species of mesopredators may then face increased predation pressure which can threaten their long-term viability. This has been directly demonstrated in

the extinction of avian fauna (Crooks and Soulé 1999) and Australian marsupials (Johnson et al. 2007).

Apex predators can play a role in biodiversity conservation by suppressing invasive mesopredators. This has been supported by studies arising from both “natural experiments” (e.g. Rogers and Caro 1998, Crooks and Soulé 1999) or retrospectively with the re-introduction of large predators (e.g. Ripple and Beschta 2007, Berger and Conner 2008). On the Australian mainland, there is evidence that the apex predator, the dingo (*Canis lupus dingo*), protects smaller native marsupials from decline and extinction through the suppression of invasive red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) (e.g. Smith and Quin 1996, Johnson et al. 2007, Letnic et al. 2009b, Brook et al. 2012). Nearly 50% of all mammal extinctions worldwide over the past two centuries have occurred in Australia (Short and Smith 1994) and the majority of these extinctions have occurred in the prey size range of introduced mesopredators. Of placental native rodents, 19% are now extinct compared with 6% of the total Australian mammalian fauna. Feral cat abundance is the greatest predictor in the declines of the smallest species and where dingoes were present, declines are less severe (Smith and Quin 1996). The effects of novel introduced predators on prey species may be more severe than native predators, and may be due to deficient avoidance behaviours and naivety of prey species (Salo et al. 2007).

Disease induced decline of the Tasmanian devil (*Sarcophilus harrisii*) provides a unique opportunity to investigate the impact of an ongoing decline of an apex predator on a mammal community. On Australia's island state of Tasmania, the Tasmanian devil is the effective mammalian apex predator and the largest extant marsupial carnivore following the extinction of the thylacine (*Thylacinus cynocephalus*), which was last officially recorded in the mid

1930's. Devils are threatened with extinction in the wild from a consistently fatal transmissible cancer termed devil facial tumour disease (DFTD), first observed in 1996 (McCallum et al. 2009). Population decline of devils is rapid and severe within a few years of DFTD arrival into an area (McCallum et al. 2007, McCallum et al. 2009). Regions subject to disease for extended periods have suffered population declines in excess of 95% and the disease has now spread to more than 75% of the devil's current geographic range (Save the Tasmanian Devil Program, 2012). To date there has been no indication of population recovery, although devils still persist in diseased regions at low densities. Evidence suggests that the population decline of Tasmanian devils has led to the competitive release of feral cats and a concomitant decline in eastern quolls (*Dasyurus viverrinus*) (Chapter 2). This indicates that devils may indirectly protect eastern quolls through suppression of larger mesopredators.

Tasmania retains an intact community of native marsupial carnivores and prey species as well as supporting several introduced species at different trophic levels. In the multi-level top-order carnivore guild, the feral cat and the native marsupial spotted-tailed quoll (*Dasyurus maculatus*) are larger mesopredators which may compete as they are similar in body size and prey species composition (Dickman 1996). Prey of these mesopredators comprises largely small and medium-sized mammals (Belcher 1995, Dickman 1996). The smallest carnivore in the guild, the native marsupial eastern quoll, may be subject to intense competition and predation from spotted-tailed quolls and cats (Jones et al. 2004). There is ecological and evolutionary evidence of competition within the native carnivore guild, including diet overlap and aggressive interference competition, with spotted-tailed quolls expected to experience the most extensive competition (Jones 1997, Jones and Barmuta 1998). Apart from the extinct thylacine and irrespective of the presence of the introduced cat and the recent illegal

introduction of the red fox (*Vulpes vulpes*) (Sarre et al. 2012), no major declines or extinctions had been recorded in the Tasmanian mammal fauna, until the emergence of DFTD.

In this chapter I investigate the effects of the decline of the Tasmanian devil, an apex predator, on the abundance and activity of mammalian mesopredators and secondary effects on their terrestrial prey. First, I evaluate the species composition of communities to determine whether there is movement towards a more invasive, homogenised state in areas of long-term devil loss. Second, I examine whether ecologically similar native and introduced species are responding differently to the decline in devil populations. Third, I assess if there is evidence for mesopredator release of feral cats and spotted-tailed quolls in response to devil decline in both abundance index measures and the timing of their activity. Lastly, I test whether the presence of certain predator species affects the occurrence of their prey species. I address these specific community and species responses by conducting rapid snapshot surveys across Tasmania. The extensive spatial scale encompasses the full range of DFTD arrival times, which represent a proxy for devil population decline over time.

3.4 METHODS

3.4.1 DFTD arrival regions and years since disease arrival

Because of the consistency of devil population decline following DFTD arrival (McCallum et al. 2007, McCallum et al. 2009), the number of years DFTD has been present in an area is a reasonable proxy for the extent of decline in the local devil population. It is also a measure of the length of time devil populations have been suppressed.

I partitioned the study area into three regions based on time of DFTD arrival: the early disease region in north-east Tasmania where there has been more than 90% decline in populations in the years since the mid 1990s; the mid-term disease region in the central part of the island where disease arrived from approximately 2002-2005; and the disease free region in north-west Tasmania, which still retain high densities of devils (Figure 3.1).

For more detailed analyses I established estimates of the number of years that individual survey sites had been diseased by combining extrapolations of confirmed disease from surrounding regions with expected patterns of disease spread through the landscape (McCallum et al. 2007, Save the Tasmanian Devil Program, 2012).

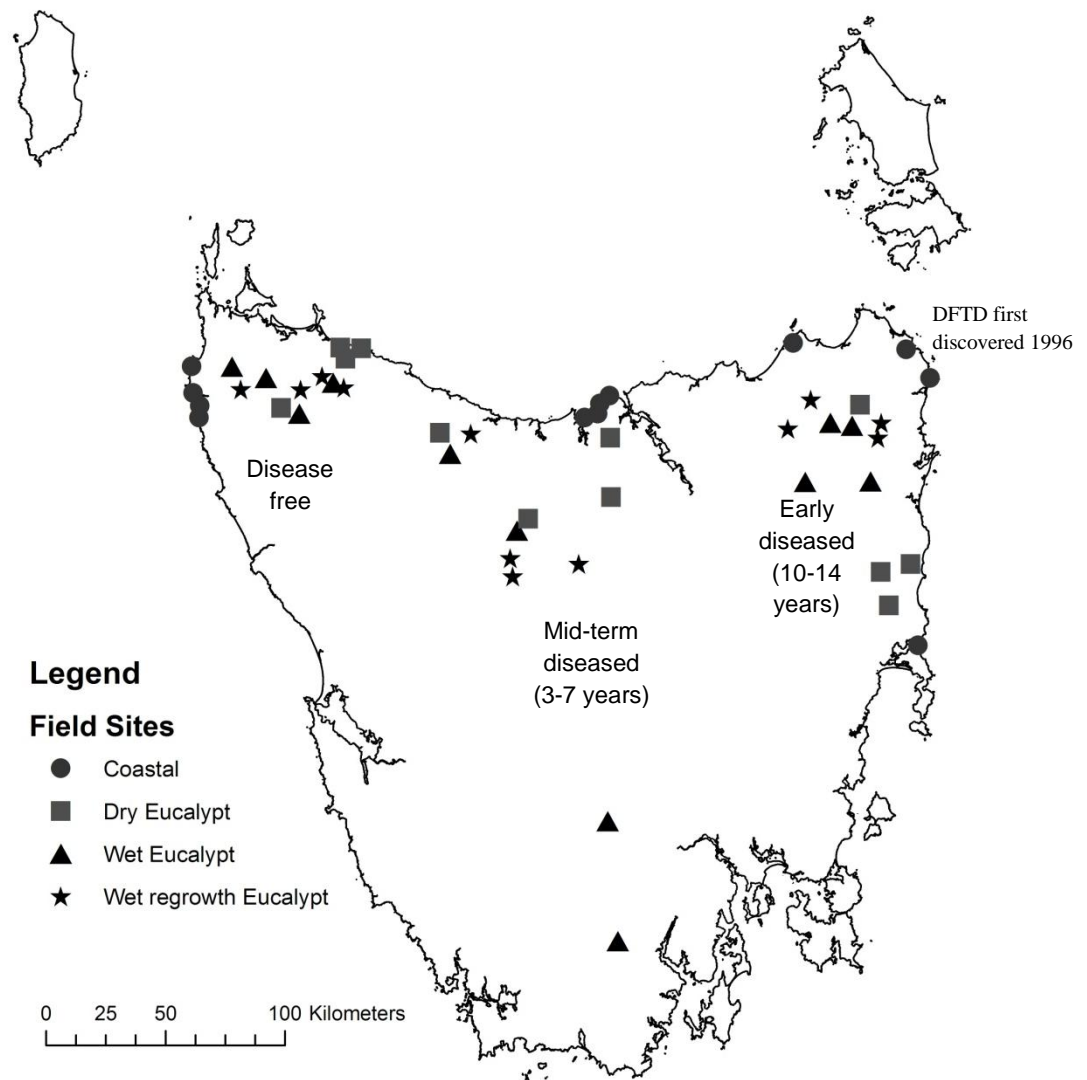


FIGURE 3.1: Field sites, categorised into vegetation type, arranged into three DFTD arrival regions: early DFTD presence; mid-term DFTD presence; and DFTD absent (disease free).

3.4.2 Site selection

I selected 48 field sites in Tasmania across the full spectrum of DFTD arrival times using ArcGIS (version 9.2), with equal numbers in each region and using predefined parameters to ensure that sites were comparable across the islands variable environment. Environmental parameters were defined to select sites to have altitude below 650m, mean annual rainfall between 1100-1600mm (Australian Bureau of Meteorology data) per year and limited to the northern part of the state to restrict variation arising from a north-south temperature gradient. This was not possible within the much more highly urbanised and agricultural mid-term DFTD region and two sites fell below the midway point of the state (Figure 3.1). Within each of the three DFTD arrival regions, four replicate sites were selected in each of four vegetation types: mature wet eucalypt forest; mature or semi mature dry eucalypt forest; regenerating wet eucalypt forest (cleared ~15-20 years prior); and coastal heath and scrubby woodland (TasVege GIS layer; Forestry Tasmania) (Figure 3.1). Each site comprised a 2km dirt track accessible by four wheel drive, that was never (i.e. behind a locked gate) or infrequently used by the public. Sites were located on public land (State Forest or National Park) except one site on private land.

3.4.3 Data collection methods

I conducted a rapid survey of sites using both hair and camera traps to obtain a relative index of abundance for devils, mesopredators and mesopredator prey species. The survey period was three nights and each site was surveyed three times over a two year period. At each site, 20 hair tubes, consisting of a PVC pipe with double-sided adhesive tape at both ends, and twenty commercially available hair funnels (Faunatech, Australia) were deployed. Half were baited to

attract herbivores (rolled oats, peanut butter and walnut oil) and half were baited for carnivores (dried liver soaked in mutton bird oil). I placed one each of a herbivore and a carnivore hair trap every 100m on alternate sides of the track, at least 20m from the road and a minimum of 10 m from each other, alternating combinations of hair trap and bait type. Hair traps were placed at ground level and secured to a log or tree ensuring that both ends of the hair tube were accessible. Hair funnels were positioned to make use of natural vegetation or microhabitat features to direct animals into the open end of the funnel. A total of 5,760 hair traps were deployed across the entire survey period. Hair samples were identified to species level using the colour, shape and patterns of cortex and medulla in cross-sectional analysis (Taylor 1985, Triggs et al. 2002).

Four infra-red motion activated cameras (Scoutguard 550) were deployed at each site; the first was placed at 250m from the beginning of the track and the remainder placed on alternate sides of the track every 500m thereafter. Cameras were placed 10-30cm above the ground and baited with both herbivore and carnivore bait (Figure 3.2). Once activated by movement, cameras were set to record a one minute of video and were then suspended for a further minute to limit repeat videos of the same individual. Individuals of devils, cats and both species of quolls are often identifiable from distinctive markings captured on camera images. Repeat videos of the same individual animal (or the same species, if individuals could not be identified) were removed, if they occurred within sixty minutes of the initial recording (Norris et al. 2010, Michalski and Norris 2011). This avoided potential bias in the data by more active individuals



FIGURE 3.2: *Photo of camera set up with bait canister*

3.4.4 Species aggregations and exclusions for analyses

The number of positive records of a species at a hair trap is an index of relative abundance for small mammal species but more accurately represents an index of activity for medium and large-sized mammals. With generally small home-ranges for rodents, and hair trap placement at a minimum 100 m apart, it is unlikely that individuals would visit more than one hair tube. For example both the endemic long-tailed mouse (*Pseudomys higginsii*) and swamp rat (*Rattus lutreolus*) have a home-range radius of approximately 45 m (Taylor and Calaby 1988, Driessen and Rose 1999). For larger mammals, individuals could visit multiple hair traps and cameras. I treated this data as an activity index and for some analyses, only presence or absence at a site was recorded. While the relative merits of indices such as these has been debated (e.g. Anderson 2001a, 2003, Engeman 2003, Johnson 2008), careful and thorough consideration of experimental design and data analysis as well as establishing the most

efficient method to meet project objectives can make indices a valuable tool for population monitoring (Engeman 2003)

Of the native medium-sized marsupials (mean body mass 600 - 1200 g), three species: the southern brown bandicoot (*Isoodon obseulus*), the eastern barred bandicoot (*Perameles gunnii*), and the long-nosed potoroo (*Potorous tridactylis*), were combined into a single category "medium mammals". Two species, the Tasmanian bettong (*Bettongia gaimardi*) and eastern quoll, have restricted geographic distributions, limiting their use in any spatial analysis as they do not occur across the range of DFTD arrival sites. Bettongs are absent from the entire western half of the state (Rounsevell et al. 1991). Eastern quolls are extremely rare or absent in much of the disease free north-west as well as some of the mid-term diseased sites (Rounsevell et al. 1991, Jones and Rose 1996) (Figure 3.5).

I aggregated the hair trap data for small rodent species into two classes: "native" and "introduced" small mammals. The hair of some closely related species can be difficult to distinguish due to morphological similarities (Taylor 1985, Lindenmayer et al. 1999). This is true for rodent species which can also be difficult to accurately identify from camera videos due to video clarity, being obscured or concealed by microhabitat, and the speed at which they move. Native small mammals in Tasmania comprise five species of native rodents, and three species of carnivorous marsupials. Of these native species, I only identified hair from the long-tailed mouse and swamp rat. Black rats (*Rattus rattus*) were the only introduced rodents included in the analysis. I excluded house mice (*Mus musculus*) because a plague in 2010 in the north eastern and middle parts of the state might have been associated largely with a wetter than average winter and a warm summer (Bureau of Meteorology data) providing ideal breeding conditions for the house mice (Kempton 2010). This distorted the data with very

high densities in certain areas (Figure 3.5). Introduced brown rats (*Rattus norvegicus*) were not detected in any samples.

3.4.5 Statistical analysis

Community composition

To assess whether species composition and the extent of community homogeneity varied with DFTD region I applied nonmetric multidimensional scaling (nMDS) with the Bray-Curtis dissimilarity matrix (using library ‘vegan’ in R 2.11.0). The species composition data were derived from the number of positive hair traps for each species for each of the three replicate surveys from all field sites. The data were standardised by applying a $\log(x + 1)$ transformation to reduce the influence of the most abundant species (Legendre and Legendre 1998). Species composition was analysed separately for each of the four vegetation types as habitat value for different species is expected to vary with vegetation type. Each individual survey of a field site is represented by a symbol denoting the DFTD arrival region to allow visualization of evidence for clustering of sites located within the same region. I applied a spider diagram to connect each point to the centroid of the associated DFTD region.

Next, I conducted a permutational multivariate analysis of variance (Anderson 2001b) on the composition data for each of the four vegetation types with the Bray-Curtis dissimilarity matrix as the response variable (using library ‘vegan’ in R 2.11.0). For this analysis, the number of years that a site had been diseased was used as the predictor variable. I restricted the permutations to within each field season to account for the randomization of the repeated measures from the three repeat surveys of each field site.

Invasive species community composition

I assessed whether introduced species, considering all trophic levels, comprised a greater proportion of the overall community composition in response to declining apex predator populations. Introduced species were defined as black rats and feral cats. First, I plotted the proportion of hair traps that were positive for introduced species hair within each DFTD arrival region. Second, I modelled whether the positive records from the hair traps for all species were from an introduced species or not with the number of years that a site had been diseased and vegetation type as predictor variables. The vegetation variable was used to account for the differences in community composition expected across the four vegetation types. I used generalized linear mixed models (GLMMs) with a binomial error structure and logit link function (using the ‘lme4’ library in R version 2.11.0). These models included random effects in the linear predictor to account for the repeated nature of the surveys of each site across three distinct field seasons. To assess the support for the four alternative models I used the weights (w_i) derived from small sample corrected Akaike Information Criterion (AICc), where the weight provides the relative support for each model (Burnham and Anderson 2002).

Mesopredator activity index and relative abundance of prey species

I assessed whether there were discernible differences in the abundance index of each species in relation to 1) the length and extent of devil population decline; 2) the occurrence/abundance of competitively dominant species, predators or prey. For all species except cats, the response variable was the proportion of total hair traps deployed that were positive for the species of

interest, for each individual survey of a site. For feral cats I used presence/absence data as only two sites had more than one trap positive for cat hair.

For all models, the predictor variables were number of years since DFTD arrival, vegetation community, and the occurrence (presence-absence), abundance or activity of other species which may have a direct effect on the species of interest. The devil activity measure from hair traps and the years since DFTD arrival were inversely correlated (Spearman's rank correlation coefficient = -0.69) and therefore I used years since DFTD arrival as the predictor variable in all analyses to represent apex predator populations. This variable represented both devil population at the time of the survey and the length of time devil populations had been declining, in contrast to the activity measure from hair traps which only represents devil populations at the time of the survey, albeit at a more localised scale. To reduce over-fitting, I limited the number of species used as predictor variables to two, using those predators or prey species I considered likely to have the most influence on the species being analysed. No other species used as predictor variables for devils. For the larger mesopredators, the feral cat and the spotted-tailed quoll, I used predictor variables of native and introduced small mammals. These mesopredator species were used as the predictor variables for their prey species, the medium mammals and the native and introduced small mammals. Correlation of predictor variables was assessed prior to analyses using Spearman's rank correlation coefficient.

I tested for zero inflation (using 'glmmADMB' package in R) for each species by fitting zero inflated GLMMs with random effects to the null models. The fit of the zero inflated binomial model against a binomial GLMM was assessed using AICc. There was no evidence for zero inflation for any species and all species that had many zeros in the data had low mean:variance ratios.

I used GLMMs with a binomial error distribution and logit-link function to fit the models with the random effects of field season and repeat site survey as for the previous analyses. A set of alternative models were fitted to species data, with the most parsimonious model selected on the basis of its AICc. All combinations of models were tested using the four predictor variables for each species. The relative importance of each explanatory variable was quantified by summing the weights of all models containing the variable (Burnham and Anderson 2002, Rhodes et al. 2006).

Mesopredator activity time

I assessed mesopredator activity times in relation to devil populations by using the time stamps from the motion activated remote cameras. To ascertain if there were differences among disease regions in whether activity was focused towards sunset or sunrise, I separated the videos into the appropriate DFTD arrival region and determined whether the time of the video taken was closest to sunset or sunrise for all species within the carnivore guild. I then applied a Fisher's exact test to the data for each species. The restricted geographic distribution for eastern quolls limited analysis for this species to the early and mid-term diseased regions.

Further, I determined whether the activity time of mesopredators could be predicted by the occurrence of devils at the site within the same survey period (three days). To account for different day length throughout the year I transformed the data to a scale on which sunrise and sunset were set to 0 and the transformed time value of each data point was the number of hours the activity that occurred relative to sunrise or sunset. Night time activity prior to sunrise or after sunset was given negative values and daylight given positive values. Using this transformed data as the response variable for the native spotted-tailed quoll and eastern

quoll I fitted GLMMs with Gaussian error structure and identity link function with site and field season as random factors (using the ‘lme4’ library in R version 2.11.0). Limited data for feral cats precluded analysis for this species. As predictor variables I used the presence or absence of devils at the site during the survey period, a factor indicating whether the activity was closest to sunset or sunrise, and the disease region as an interaction term with devil presence to determine whether the presence of a devil affects activity differently in different DFTD arrival regions. The presence of a devil in a long-term suppressed population may have more or less of an effect than the presence of a devil in a higher density devil population. There were five models assessed using the two predictor variables, their interaction and the null model. Correlation between predictor variables was assessed using Spearman’s rank correlation coefficient. As for previous analyses, I used weights (w_i) derived from small sample corrected Akaike Information Criteria (AICc).

3.5 RESULTS

3.5.1 Community composition

Non-metric multidimensional scaling indicated that a large proportion of sites within the early diseased region were closely related and therefore clustered together in three of the four vegetation types (Figure 3.3). The signal was strongest in the dry eucalypt forest sites and coastal woodland scrub. This pattern was not evident for either the mid-term or the disease free sites. Permutational multivariate analysis of variance corroborated the findings from the nMDS, indicating that community composition was significantly associated with the number of years the site had been diseased in three vegetation types, with the strongest effects in dry eucalypt and coastal vegetation types (dry eucalypt forest sites, $R^2 = 0.102$, $p = 0.001$; coastal woodland scrub, $R^2 = 0.113$, $p = 0.002$; wet eucalypt mature forest, $R^2 = 0.088$, $p = 0.02$). There was no evidence of clustering or association with the number of years diseased in wet eucalypt regeneration sites ($R^2 = 0.037$, $p = 0.301$). The tighter clustering of early diseased sites in comparison with disease-free sites may represent a tendency towards different and possibly more homogenised mammal communities.

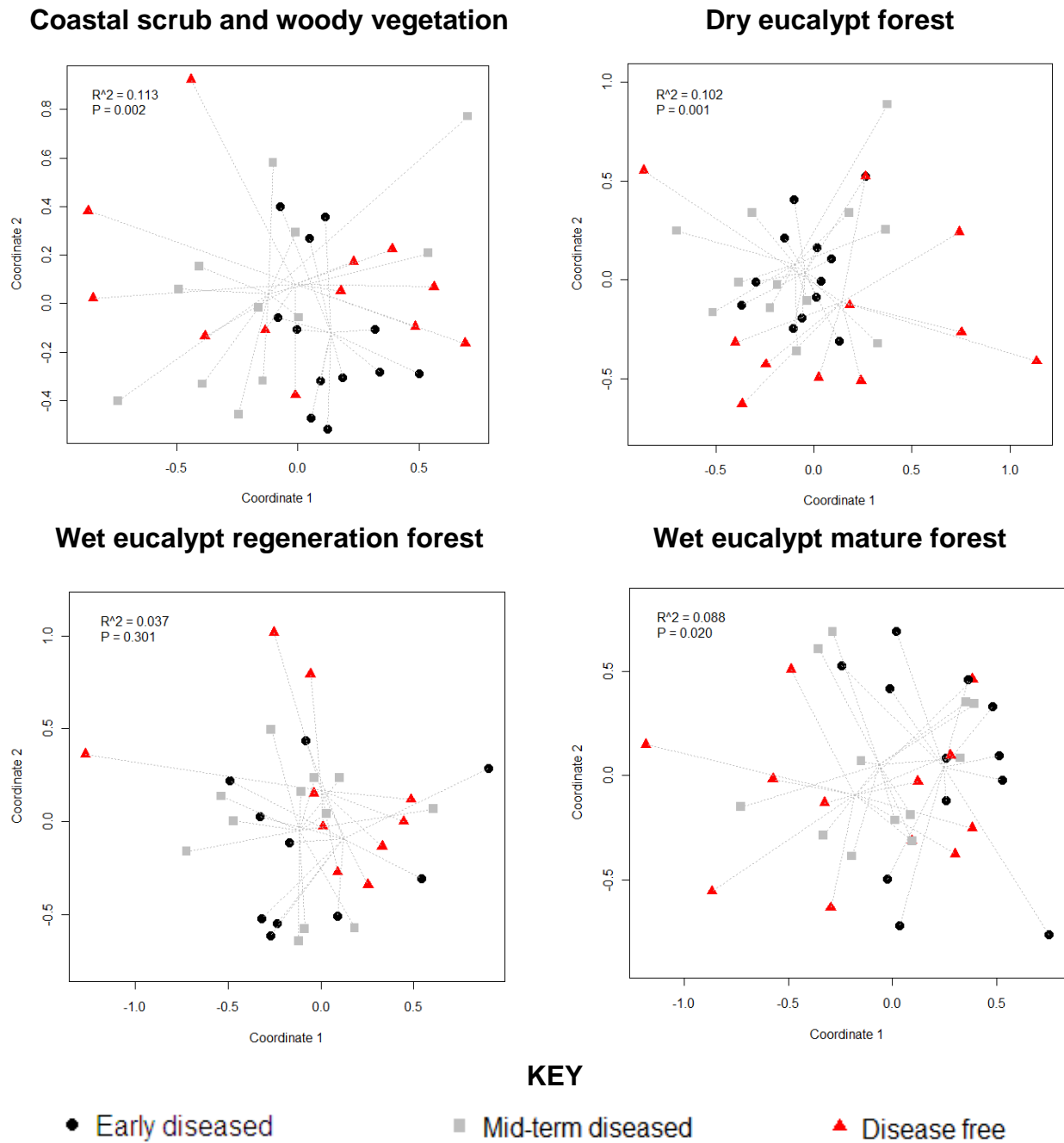


FIGURE 3.3: Non-metric multidimensional plot for species compositions across the three DFTD regions of early disease, mid-term disease and regions which are currently disease free. Results for the permutational multi variate analysis are shown inside the plot for each vegetation type.

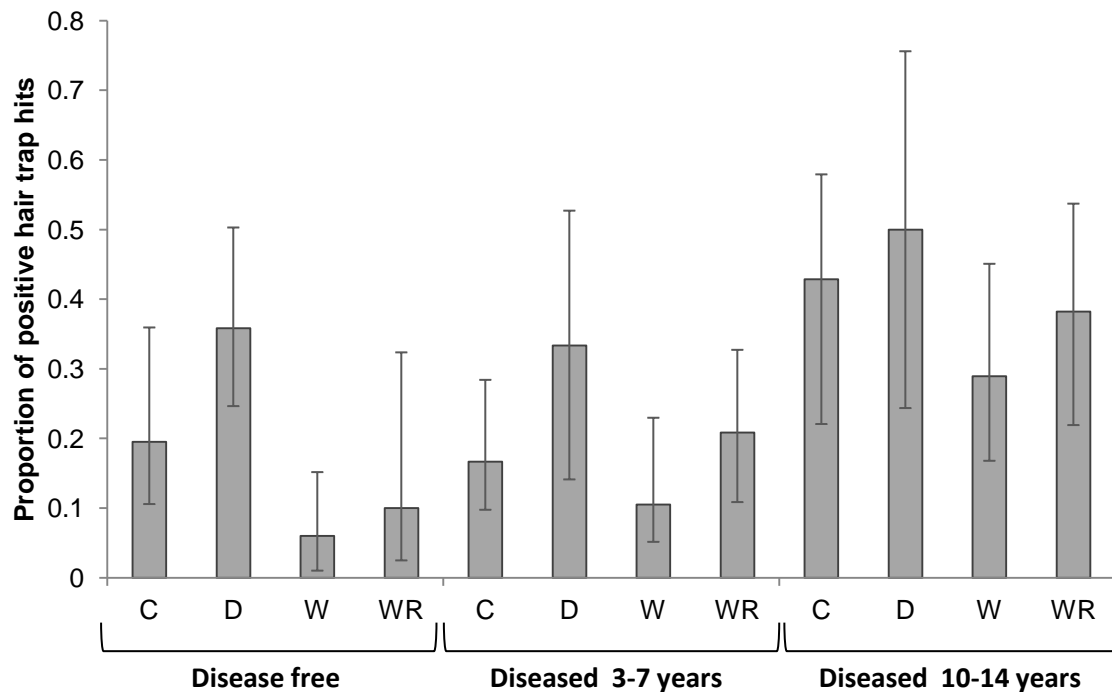


FIGURE 3.4: *The percentage of positive hair traps which were identified as an introduced species, based on mesopredator and their prey species. Error bars represent the 95% binomial confidence intervals. C = coastal woodland scrub, D = Dry eucalypt forest, W = Mature wet eucalypt forest, WR = Wet eucalypt rengerated forest*

3.5.2 Invasive species community composition

The data suggest that at least some of the differences in community composition between DFTD arrival regions may arise from the variable dominance of introduced species. There is a trend towards higher proportions of the species recorded in hair traps to be introduced species in areas diseased the longest, for all vegetation types (Figure 3.4). Introduced species were also detected at a greater number of sites in the early diseased region than in the disease free

region with intact devil populations. The GLMM results indicated that years since disease arrival and vegetation type were important in explaining the number of introduced species identified in positive hair traps with the best supported model containing both of these variables and with a weight of 66% (Table 3.1). The second model, containing the single predictor variable of years since disease arrival, was not significantly different from the best supported model (falling within ΔAICc of less than two) and accounted for 32% of the weight within the candidate model set.

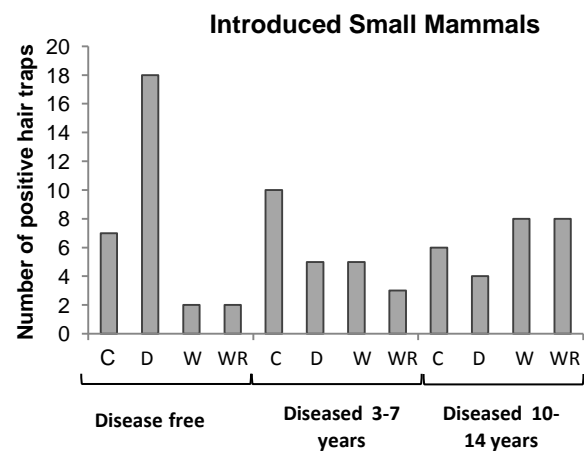
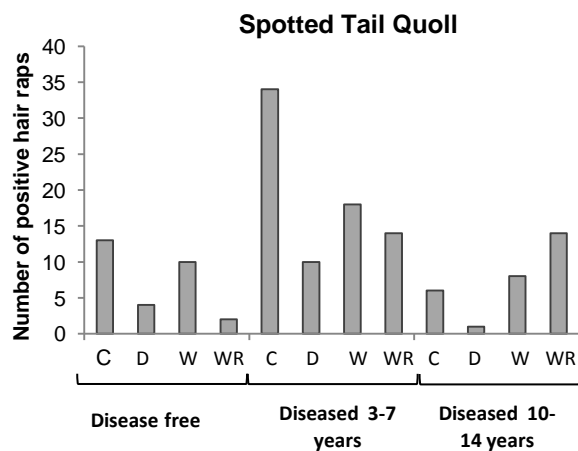
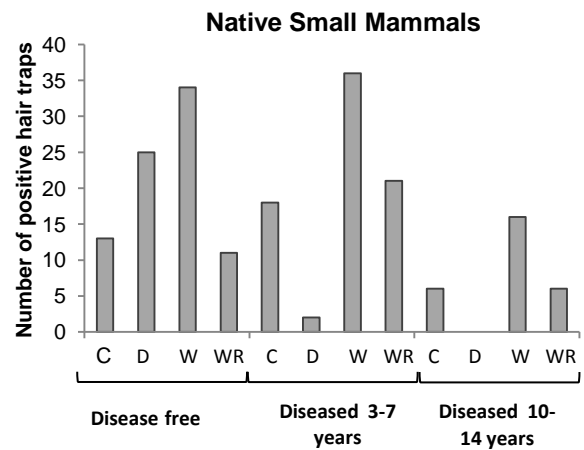
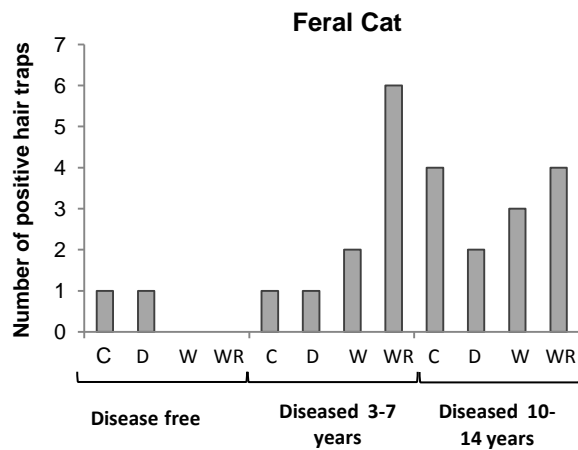
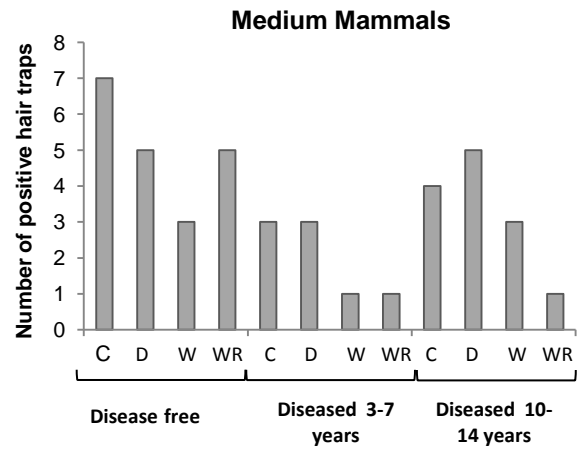
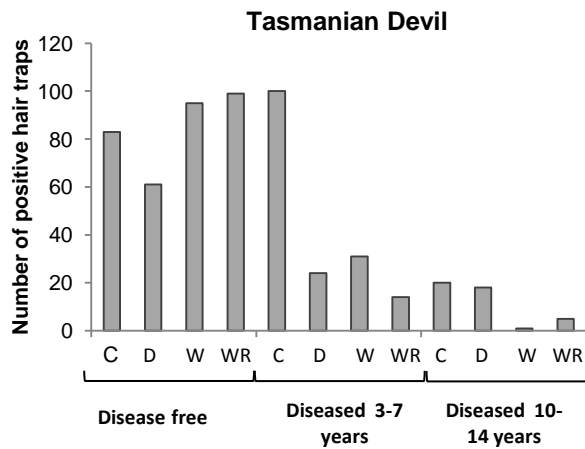
TABLE 3.1: *GLMM model outputs testing the assertion that introduced species comprise a greater proportion of the community with increasing time since DFTD arrival. k = model parameters, w_i = weight held by the model within the candidate model set.*

Parameters	Model rank	k	ΔAICc	w_i
Years diseased + Vegetation	1	4	0.00	0.66
Years diseased	2	7	1.48	0.32
Null model	3	3	7.67	0.01
Vegetation	4	6	8.88	0.01

3.5.3 Mesopredator activity index and relative abundance of prey species

The activity index for Tasmanian devils, represented by the number of hair traps in which devil hair was found, showed clear and significant declines associated with the number of years a site had been diseased (Figure 3.5). Only two models had any weight in the candidate model set: the model with the years since disease arrival as the single predictor variable ($w_i = 62\%$) and the model with years since disease arrival and vegetation type as predictors ($w_i = 38\%$) (Table 3.2a). This strong result for devils supports the use of years since disease arrival as a predictor variable representing the extent of devil population decline and the use of hair trap rates as a proxy for activity of species.

The feral cat activity index was strongly and positively linked with the length of time sites had been diseased. This relationship is clearly visible from the plots of the number of hair traps in which hairs of each species were recorded (Figure 3.5). The GLMM model with the number of years a site had been diseased as a single predictor variable had the highest weight ($w_i = 39\%$) and the relative importance of this variable, representing the weight of all models containing it as a predictor, was 93% (Table 3.2b). Feral cat activity was positively associated with the presence of both native and introduced rodent prey species (two additional models within ΔAIC_c of two), although the relative importance of these predictor variables carried lower weight at 33% and 28%, respectively (Table 3.2b).



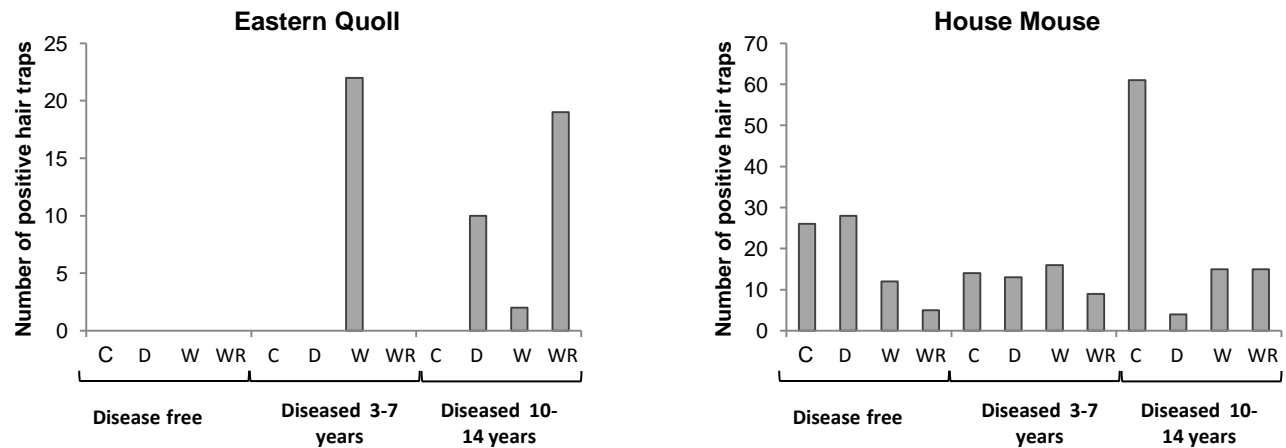


FIGURE 3.5: Number of positive hair traps as a measure of activity index or relative abundance of species in different habitat types, across the range of DFTD arrival times. C = coastal woodland scrub, D = Dry eucalypt forest, W = Mature wet eucalypt forest, WR = Wet eucalypt renerated forest. Medium mammals = southern brown bandicoot, eastern barred bandicoot and long-nosed potoroo; Native mammals = swamp rat and long-tail mouse; Introduced small mammals = black rat

The most importance variable explaining activity of the similar-sized, native spotted-tailed quoll was larger populations of introduced small mammals. The model containing this single predictor variable carried the highest weight ($w_i = 25\%$) and this variable had a relative importance in all models of 81% (Table 3.2c). Vegetation type was also important in explaining activity of spotted-tailed quolls with a relative importance of 41%. The highest detections of spotted-tailed quolls for all vegetation types occurred in the mid-term diseased region (Figure 3.5). The lowest recorded activities were in the early diseased region of the north-east for all vegetation types except wet eucalypt regeneration forest. Neither the number of years since disease arrival nor the abundance of native rodents had a strong influence on the

spotted-tailed quoll activity index with relative importance of these variables in the candidate model set of 25% and 27%, respectively.

There was evidence for secondary effects from devil decline and increased feral cat activity on the relative abundance of mesopredator prey species but the nature of the effects varied between native and introduced species (Table 3.3). For native medium mammals, the lowest recorded number of positive hair traps for all vegetation types were in the mid-term disease region (Figure 3.5). The variable with the highest importance was the activity index of the spotted-tailed quoll (51%) followed by that of the feral cat (42%) and both were negatively associated with medium mammal populations (Table 3.3a). The model with spotted-tailed quolls as a single predictor variable had the highest model weight ($w_i = 0.16$), however this was not significantly different from five other models, including the null model ($w_i = 0.15$).

TABLE 3.2: Most parsimonious GLMM models and parameter estimates for top order carnivores for hair trap data analysis with $\Delta AICc$, k = parameters, model weight (w_i) and model coefficient estimates with ± 1 SE. Dashed lines highlight the most heavily weighted models from the candidate model set within $\Delta AICc$ of two. Parameter estimates are included for these models only, with X denoting the presence of variables in lower ranked models; not all models are shown. Relative importance of variables represents the weight of all models which contain that variable. Vege type parameters are against coastal scrub, W = Wet mature eucalypt forest, D = Dry eucalypt forest, WR = Wet eucalypt regeneration forest. NA = Not assessed for that species.

Model rank	k	$\Delta AICc$	w_i	Parameter estimates			Small mammal introduced	Small mammal native	
				Intercept	Years diseased	Vege Type			
a) Tasmanian devil									
1	4	0.00	0.62	-1.69±0.21	-0.23±0.03	D:-0.50±0.37 W:-0.75±0.37 WR:-0.76±0.38	NA	NA	
2	5	1.24	0.38	-1.22±0.29	-0.22±0.03				
3 (Null)	3	43.11	0.00	-3.09±0.22					
4	4	44.57	0.00	X	X				
Relative weight of variable (%)					100	38			
b) Feral cat									
1	4	0.00	0.39	-2.64±0.46	0.13±0.05	0.10±0.21	X	X	
2	5	1.41	0.19	-2.88±0.56	0.14±0.05				
3	5	1.93	0.15	-2.70±0.49	0.13±0.05				
4	6	3.32	0.07	X	X				
5	5	3.87	0.06	X	X	X			
6	6	4.79	0.04	X	X	X		X	
7 (Null)	3	4.97	0.03	X					
Relative weight of variable (%)					93	14	28	33	
c) Spotted tail quoll									
1	4	0.00	0.25	-4.54±0.27	D:-1.24±0.55 W:-0.32±0.53 WR:-0.73±0.53	0.17±0.08 0.18±0.08	0.03±0.07	0.17±0.08	
				-3.96±0.41					
2	5	0.56	0.19						
3	5	1.91	0.10	-4.59±0.28					
4	5	2.04	0.09		X	X			
5	6	2.72	0.06			X	X	X	
6 (Null)	3	2.81	0.06						
7	6	3.14	0.05		X	X	X		
8	4	3.59	0.04				X		
Relative weight of variable (%)					25	41	81	27	

TABLE 3.3: Most parsimonious GLMM models and parameter estimates for mesopredator prey species for hair trap data analysis with $\Delta AICc$, k = parameters, model weight (w_i) and model coefficient estimates with ± 1 SE. Dashed lines highlight the most heavily weighted models from the candidate model set within $\Delta AICc$ of two. Parameter estimates are included for these models only, with X denoting the presence of variables in lower ranked models; not all models are shown. Relative importance of variables represents the weight of all models which contain that variable. Vege type parameters are against coastal scrub, W = Wet mature eucalypt forest, D = Dry eucalypt forest, WR = Wet eucalypt regeneration forest.

Model rank	k	ΔAICc	w _i	Parameter estimates				
				Intercept	Years diseased	Vege Type	Feral cat	Spotted quoll
a) Medium mammals								
1	4	0.00	0.16	-5.11±0.30				-0.18±0.14
2 (Null)	3	0.04	0.15	-5.23±0.26				
	3	5	0.49	0.12	-5.02±0.30		-0.74±0.65	-0.18±0.14
4	4	0.56	0.12	-5.13±0.26			-0.73±0.65	
5	4	1.42	0.08	-4.92±0.35	-0.03±0.04			-0.18±0.14
6	6	1.53	0.07	-5.05±0.33	-0.03±0.04			
7	5	2.30	0.05		X		X	X
8	6	2.41	0.05		X		X	
9	5	2.74	0.04			X		X
Relative weight of variable (%)					31	20	42	51
b) Native small mammals								
1	5			-3.44±0.37	-0.10±0.03	D:-0.98±0.51 W:0.87±0.44 WR: 0.04±0.46		
2	6	2.07	0.19		X	X	-0.09±0.26	
3	6	2.16	0.18		X	X		0.01±0.05
4	7	4.26	0.06		X	X	X	X
Null	12	13.85	0.00					
Relative weight of variable (%)					96	98	26	25
c) Introduced small mammals								
1	4	0.00	0.35	-5.08±0.23				0.13±0.06
2	5	1.09	0.20	-5.16±0.25			0.39±0.38	0.14±0.06
3	5	2.00	0.13		0.02±0.04			0.14±0.06
4 (Null)	3	2.43	0.10	X				
5	6	3.22	0.07		X		X	X
6	4	4.14	0.04				X	
7	4	4.49	0.04		X			
Relative weight of variable (%)					25	7	34	80

The number of years that disease had been present had a considerable negative effect on small native mammal populations; the relative importance of this variable was 96% (Figure 3.5, Table 3.3b). Vegetation type was also important for these species with a relative importance of 98%. The single model in the final model set contained both these predictor variables and held 52% of the weight in the candidate model set. The highest hair trap rates were in mature wet eucalypt forest (Figure 3.5).

The number of years a site had been diseased, activity index of feral cats and of spotted-tailed quolls were all positively associated with introduced small mammal populations. These three variables were included in the final set of three models that were within an AICc of two (Table 3.3c). The relative importance for the spotted-tailed quoll as a predictor of introduced rodent abundance was the highest at 80%, followed by a less substantial influence of feral cats at 34%. Vegetation type was not important in explaining introduced small mammal populations in these models.

3.5.4 Mesopredator activity times

Devil activity peaked within the hours of darkness with most activity just after sunset, but with another peak a few hours before dawn (Figure 3.6). There were substantially higher activity levels of devils in the disease free regions compared to early diseased regions. This is consistent with the substantial disease-induced population declines.

TABLE 3.4: *Activity time data available on devils and each mesopredator species by region with the number of detections closest to sunset or sunrise. The data represents the total number of camera videos recorded with repeat animals removed (see Methods). Results of the Fishers Exact tests compare differences in activity between sunrise and sunset among disease regions.*

Species	Video closest to:	Number of videos by region			Fishers test p-value
		Early diseased	Mid diseased	Disease free	
Tasmanian devil	Sunrise	13	42	84	0.402
	Sunset	12	69	135	
Feral cat	Sunrise	4	3	5	0.376
	Sunset	2	7	3	
Spotted-tailed quoll	Sunrise	13	25	13	0.552
	Sunset	9	22	6	
Eastern quoll	Sunrise	8	14	NA	0.011*
	Sunset	20	7	NA	

Spotted-tailed quolls were strongly crepuscular with a substantial proportion of diurnal activity, particularly in the disease free region in the north-west where devil abundance was highest (Figure 3.6). Figure 3.6 suggests that the peak of spotted-tailed quoll activity shifted towards night time as devil populations declined, with the highest activity levels recorded in the mid-disease region. This is supported by the GLMM analysis (Table 3.5a), which detected some differences in activity times in the presence of devils. Three of the top four candidate models for spotted-tailed quoll activity contain either or both of the predictor variables of devil presence and disease region. The response of spotted-tailed quolls to the occurrence of devils may also vary with DFTD region, as indicated by the interaction term within the top

models. The null model was also within the top candidate set of models, ranking third and within a $\Delta AICc$ of two, so these conclusions need to be interpreted with caution.

Eastern quoll activity was strictly nocturnal across both disease arrival regions with no activity recorded after sunrise or prior to sunset (Figure 3.6). The total level of activity was relatively consistent across both regions. The null model was the most parsimonious model in the GLMM analyses of eastern quoll activity. Models containing the single predictor variable of devil occurrence at the site, and this variable in combination with disease region, also fell within $\Delta AICc$ of two indicating that they had similar support to the null model (Table 3.5b).

Results from the Fisher's exact test (Table 3.4) indicated that eastern quolls were significantly more active in the hours before sunrise in the mid region and in the hours after sunset in the early region, where devil populations have been suppressed the longest ($p = 0.011$). However, for the larger mammalian mesopredators – the cat and spotted-tailed quoll – the Fisher's exact test (Table 3.4) indicated no significant difference in activity around sunrise or sunset across different DFTD arrival regions. The data for feral cats were too sparse to draw any strong conclusions regarding activity times.

TABLE 3.5: *GLMM model analysis for the activity times of native mesopredators, the spotted tail quoll and eastern quoll, showing $\Delta AICc$, model weight (w_i) and model coefficient estimates with ± 1 SE. Only the top candidate models which are within $\Delta AICc$ of two are included in the table. Disease region estimates are compared against the disease free region for spotted tail quolls, and the early region for eastern quolls who are not present in the disease free region.*

Top model Set	Model selection				Parameter estimates			
	Model rank	k	$\Delta AICc$	w_i	Intercept	Devil present	Region (Early)	Region (Mid)
a) Spotted tail quoll								
Devil present	1	4	0.00	0.22	-1.74 \pm 0.62	1.32 \pm 0.76		
Devil present*Region	2	8	0.09	0.21	-5.50 \pm 1.84	devil:region (early): 4.55 \pm 1.96 devil:region (mid): 3.89 \pm 2.03		
Null	3	3	0.56	0.17	-0.91 \pm 0.37			
Devil present + Region	4	6	1.71	0.09	-1.40 \pm 1.01	1.49 \pm 0.81	0.24 \pm 1.01	-1.16 \pm 0.89
b) Eastern quoll								
Null	1	3	0.00	0.29	-3.31 \pm 0.39			
Devil present	2	4	1.05	0.17	-3.04 \pm 0.43	-0.99 \pm 0.43		
Devil present + Region	3	5	1.84	0.11	-3.38 \pm 0.32	-1.21 \pm 0.63	NA	1.09 \pm 0.56

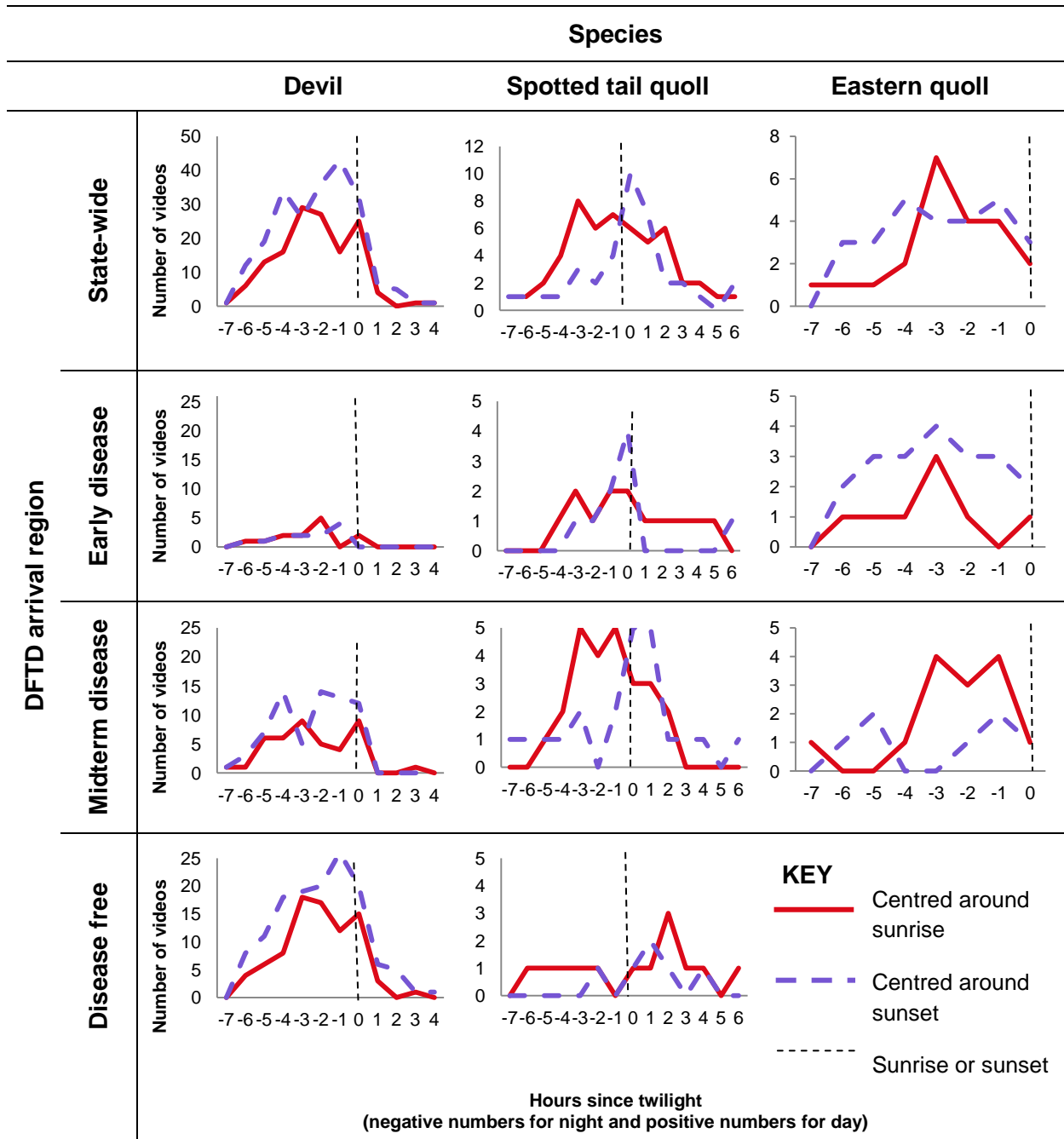


FIGURE 3.6: Activity time plots for native mesopredators and devils. The data for time of activity was transformed to the number of hours since twilight with sunrise and sunset set at zero. Night time had negative values and day time positive values.

3.6 DISCUSSION

Tasmania's mammal community is exhibiting signs of extensive and diverse changes following disease-induced apex predator decline. The evidence supports the hypothesis that the Tasmanian devil plays a keystone role and exerts top-down regulation on the mammal community. In three of the four vegetation communities assessed there was evidence of changes in species composition with increasing time since disease arrival. In particular, invasive species comprise a significantly higher proportion of the total community composition where devil populations have been suppressed by DFTD. There is strong support for mesopredator release of feral cats, with increasing activity levels correlated with an increasing number of years since DFTD arrival. Evidence for mesopredator release in the large native mesopredator, the spotted-tailed quoll, is less clear and may be countered by competition from the feral cat. Spotted-tailed quolls do appear to avoid devils by altering their periods of activity to times of day that devils are less active when devils are at higher densities. There is evidence that all native prey species are detrimentally affected by the presence of larger mesopredators or years since DFTD arrival, in contrast to introduced small rodent populations which are positively associated with the occurrence of mesopredators. This study provides evidence that communities are more homogenised and invasive-driven in areas of long-term devil decline, which could have adverse effects for naive native species.

The loss of an ecologically functional apex predator leading to a more invasive state has been demonstrated previously (Wallach et al. 2010) and may be a common consequence of apex predator loss (Estes et al. 2011). Invasive species have successfully colonised and now dominate landscapes in most parts of the world, due to both the intentional and accidental release of beneficial and pest species by humans (Kolar and Lodge 2001, Didham et al. 2005).

The results here provide strong evidence that devil decline is reducing the diversity of the Tasmanian mammal community, which is shifting towards a more invasive-dominated state. This is demonstrated with the introduced feral cat and black rat comprising a significantly higher proportion of the total community composition where apex predator populations have been suppressed by DFTD. Once competitive and predatory suppression is lifted, invasive species may be able to extend their ecological dominance. Invasive species, compared with their native counterparts, may have higher capability for dispersal and be more adaptable to changing environmental conditions, particularly in response to anthropogenic influences (Didham et al. 2005) potentially becoming the dominant force in driving community structures (Croll et al. 2005).

The mesopredator release hypothesis predicts that the removal of suppressive competition from devils would lead to an increase in both the invasive feral cat and the native spotted-tailed quoll. There is evidence from long-term spotlighting records of an increase in feral cats in some ecosystem types following devil decline (Chapter 2). Using a different methodology with different limitations and advantages, this study provides further corroborative support for mesopredator release of this invasive species. The higher activity index of feral cats in areas of long-term devil decline, and the strong positive correlation with the number of years since DFTD arrival provides evidence of top-down suppressive control by devils.

Following apex predator loss, behavioural changes, such as increased activity, altered activity times and changes in habitat use may occur immediately. As these behaviours are linked to fitness, they can translate over time to changes in population vital rates and population demography (Morris et al. 2009). The higher activity index for feral cats may be associated with increasing abundance, following well over a decade of diminished competitive pressure

from devils. These results have parallels with the situation on the mainland of Australia, where reduction in the population of a different apex predator, the dingo *Canis lupus dingo*, can permit feral cats to relax spatial and temporal partitioning behaviours by which they avoid dingoes and thus take greater advantage of prey availability and thus promote increases in abundance (Brook et al. 2012).

In contrast to the response of feral cats to devil decline, the activity index of the similar sized spotted-tailed quoll is closely related with the abundance of prey species. However, there is an indication that spotted-tailed quolls avoid devils by altering their activity times at different devil densities. Unlike devils, which are strictly nocturnal, figure 3.6 and table 3.4 show that spotted-tailed quolls shifted their activity towards more diurnal hours where devil densities were high and there was evidence for activity changes on a local and regional scale. The activity observations for spotted-tailed quolls could also be indicative of competitive suppression by feral cats. This assertion remains tentative, but some evidence to support it arises from the fact that the spotted-tailed quolls have the lowest activity index levels in the early diseased region where devil populations are lowest and cat densities are highest. The highest activity index levels are in the mid-term diseased region where devils have declined only recently and feral cat density is lower than in the early diseased region. These patterns suggest that spotted-tailed quolls may respond positively to declining devil populations (mesopredator release) as indicated by their behavioural changes, but may be outcompeted by increasing populations of feral cats. Spotted-tailed quolls have similar dietary requirements (Dickman 1996) and overlap spatially with feral cats (Glen and Dickman 2008). Any increase in populations of feral cats may increase interference and exploitative competition on spotted-tailed quolls (Glen and Dickman 2008). Unfortunately, to date there has been no experimental

examination of competitive interactions between feral cats and any native predator (Dickman 1996).

An increasing mesopredator population will increase predation pressure on prey, potentially causing population declines and extinctions in native species (Crooks and Soulé 1999, Johnson et al. 2007, Letnic et al. 2009b). In this study, the relative abundance of all mesopredator prey species correlates with devil decline or higher predation pressure, although the direction of the response varies between native and introduced species. Abundance of native small mammals is negatively associated with number of years since disease arrival and they appear to be facing substantial population declines and have the greatest magnitude of response to declining devil populations relative to other prey species. The link between increased activity of the larger mesopredators, as measured from the hair traps, and small mammal decline is compelling but it is difficult to distinguish between causes and correlates of decline for these species. Medium mammals respond negatively to the presence of larger mesopredators and show a decreasing trend in relation to time since DFTD arrival. In contrast to the native species, introduced small mammals are positively linked with the occurrence of larger mesopredators and years since DFTD arrival. The difference in response of native and introduced prey species could arise for two reasons. First, native species are often naïve to introduced predators, making them considerably more detrimental to prey species than native predators (Salo et al. 2007). Evidence of this naiveté has been demonstrated in two native Tasmanian mammals: eastern quolls and swamp rats (*Rattus lutreolus*) (Jones et al. 2004b, McEvoy et al. 2008). Second, introduced species may be competitively dominant over native species. Damaging effects of black rats on native small mammal fauna have been revealed in some ecosystems (e.g. Morris 2002), but not in others (e.g. Ganzhorn 2003) indicating that the

effects of black rats may be context dependent. Either way the varied responses of prey species are suggestive of invasive species driving community structure in areas of long-term devil decline. This could place all five native rodent species and other small mammals in Tasmania at risk of local declines or extinction. Almost 20% of placental native rodents have gone extinct in Australia and the abundance of feral cats is the major predictor in declines of the smallest of these species; yet where apex predators are present, declines are less severe (Smith and Quin 1996).

The restricted geographic range of the eastern quoll in eastern Tasmania precluded its use in most of the analyses, but there is evidence for behavioural differences between the early and mid-diseased regions. The eastern quoll, like the devil, is strictly nocturnal. When devils are scarce, eastern quolls concentrate their activity in the hours after dusk. When devil densities are high, eastern quolls are most active in the hours prior to dawn, thus avoiding the peak of devil activity just after dusk. In the previous chapter of long-term population trends there was support for the assertion that eastern quolls may be indirectly protected by devils which, competitively suppress larger mesopredators. This has been demonstrated in other multi-predator guilds (Levi and Wilmers 2011). Insufficient data were obtained on activity times of feral cats to be able to determine whether eastern quolls are avoiding this invasive mesopredator. Feral cats are known to prey on Northern quolls (*Dasyurus hallucatus*), which are of a similar size to eastern quolls, on mainland Australia (Oakwood 2000). This, along with a lack of anti-predator responses to introduced carnivores, highlights their vulnerability to any increase in predation threats (Jones et al. 2004b).

Productivity and environmental variables can influence the magnitude of responses to apex predator loss (Elmhagen and Rushton 2007, Chapter 2), the extent of which may vary for

different species. Here, there is evidence that vegetation type differentially affected the species in this study. This is not unexpected as different species favour particular habitats. Of all species, the greatest effect of vegetation was on native small mammals followed by the spotted-tailed quoll. In contrast, there was almost no vegetation effect on introduced small mammals or the feral cat. These results support theoretical predictions that successful invasive species are usually habitat generalists, which is one reason they are such successful colonisers outside their native range (Lodge 1993, Marvier et al. 2004). The greater sensitivity to vegetation type shown by native rodents suggests that they may be more vulnerable to ecosystem disruption, including habitat loss and degradation, than introduced species. To determine the effects of apex predators on lower trophic levels, the inclusion of environmental variables and heterogeneous landscapes in large-scale studies may be particularly important.

Intrinsic factors, related to methodology, and extrinsic factors including season and habitats, may affect relative abundance measures (Wilson and Delahay 2001). The analyses in this current chapter have involved using spatial variation as a proxy for temporal change. To overcome any variability over a large spatial extent, co-variables were applied in the analyses to account for seasonal and site specific variations. Whilst every effort was made to ensure that the sites were matched as far as possible for the environmental variables that were within my control, there was inevitably unavoidable variation in habitat structure, vegetation, rainfall and geology across the island. Consideration of intrinsic factors with the study design that ensured consistency of placement and deployment, as well as the relative homogeneity of environmental variables, should have provided a reliable index value for comparison of differences in the relative activity or abundance index of species.

Obtaining reliable estimates of population size in wildlife species can be challenging, particularly for nocturnal, cryptic and highly mobile species, which many carnivores are (Wilson and Delahay 2001, Claridge et al. 2004). Hair and camera trapping are non-invasive survey methods which can be deployed over large spatial scales, and can provide effective tools for fauna surveys. For large scale, multi species surveys, use of more than one survey method may be important due to the large variation in physiology and behaviour of key species surveyed. For example, the most effective hair trap type is known to vary between species (Lindenmayer et al. 1999, Mills et al. 2002).

Apex predator decline is occurring at unprecedented rates worldwide leading to more homogenised (Estes et al. 2011) and invasive-dominated community states (Wallach et al. 2010). Native species at all trophic levels in the Tasmanian ecosystem are becoming increasingly overshadowed by introduced species in areas of long-term apex predator loss due to infectious disease. Tasmanian devil facial tumour disease is perhaps the most dramatic current example of infectious disease causing large-scale population decline in an apex predator. Unfortunately, there are numerous other examples of infectious diseases impacting upon apex predators. The two mammalian orders most commonly reported in the Red List as being threatened by parasites are the carnivores and artiodactyls, with 26% of canids and 8.3% of felids being recognized as threatened by parasites (Pedersen et al. 2007). The risk that disease-induced decline of an apex predator may have far reaching effects on ecological communities is unlikely to be restricted to Tasmania.

In particular, the release of invasive mesopredators is threatening native species from increased predation and competitive pressure, conceivably shaping biodiversity composition. This evidence strengthens the notion that invasive species, and in particular mesopredators,

are a key group to benefit from apex predator loss and may become the drivers of community structures and function (Croll et al. 2005, Roemer et al. 2009). The transition towards an invasive driven state has the potential to lead to large-scale extinctions and it would be extremely difficult for the ecosystem to recover (Wallach et al. 2010). Australia has the highest recent mammal extinction rates of any continent (Short and Smith 1994), with continuing widespread and severe population declines (Ceballos and Ehrlich 2002, Woinarski et al. 2011). Tasmania may provide answers on the role of rising invasive mesopredator populations on the resilience and persistence of these native faunal communities. Apex predators worldwide which are not already extinct have been lost from large tracts of their historical ranges. Their preservation and restoration as keystone species may be critical for protecting biodiversity and promoting ecosystem resilience.

3.7 ACKNOWLEDGEMENTS

I wish to acknowledge funding from the Eric Guiler Tasmanian Devil Research Grant which allowed me to undertake this research. I would like to thank the many volunteers who aided the fieldwork and data collection for this study; the Bureau of Meteorology, Geoscience Australia and the Tasmanian Department of Primary Industries, Parks, Water and the Environment for providing the GIS data I used in this study; Forestry Tasmania staff and the Parks and Wildlife rangers; Geoff King from Kings Run who allowed me to conduct surveys on his property. I would also like to thank University of Tasmanian staff Richard Holmes who produced all the hair tubes and camera casings, and Associate Professor Leon Barmuta for statistical advice on community analyses.

Chapter 4: Changes in risk-sensitive behaviour of prey following disease-induced decline of an apex predator



4.1 ABSTRACT

Lethal and nonlethal predator-prey interactions are key components in shaping ecosystem dynamics and structuring communities. Apex predators are declining rapidly worldwide, causing the disruption of predator-prey relationships. Diminishing levels of predation risk have been linked with reduced anti-predator behaviours and increased prey populations. In Australia's island state of Tasmania, an infectious and fatal transmissible cancer is causing sustained and extensive declines of the apex predator, the Tasmanian devil, limiting its ecologically functional role in the environment. In areas of early disease arrival, more than 90% population loss has been recorded. The time since DFTD arrival into an area can be used as a proxy for the long-term devil population trend and corresponding predation risk. I utilised both a snapshot survey using hair traps and the giving up densities (GUDs) technique across the landscape of changing predation risk for the common brushtail possum to assess whether prey species of the devil are changing their activity patterns and reducing anti-predator behaviours in response to declining devil populations. There was evidence for a significantly higher index of terrestrial activity of possums in areas of long-term devil decline and a reduced time until artificial feeding patches were found. The GUDs indicated that the distance to safety, measured as an arboreal escape route, became less important as the number of years since DFTD arrival increased. Alternative predators, including avian fauna, had an important influence on some possum foraging behaviours suggesting that possums possess specific behaviours and escape mechanisms for different predators and their hunting styles. The percentage of open ground cover, expected to be related to the early detection of terrestrial predators for possums, was positively associated with lower giving up densities. The results indicated that activity, potentially related to population dynamics, and behavioural

mechanisms in possums are responding to declining devil populations and long-term apex predator absence may compromise the stability of ecosystem dynamics.

4.2 KEY WORDS

Giving-up densities; Tasmanian devil; brushtail possum; DFTD; anti-predator behaviour; apex predator loss; vigilance

4.3 INTRODUCTION

Complex lethal and nonlethal interactions between predators and prey species have the potential to shape ecosystem structures. The severe and extensive depletion of apex predators from ecosystems worldwide has disrupted predator-prey relationships and has induced cascading effects through food webs (Berger 1999, Pace et al. 1999, Schmitz et al. 2004, Heithaus et al. 2008). There is evidence for behavioural modifications (Fortin et al. 2005, Byrnes et al. 2006) and changes in community composition (Terborgh et al. 2001, Heithaus et al. 2008) following declines or extirpation of an apex predator. For prey, indirect effects of predators, mediated through changes in prey behaviour to use suboptimal habitats or activity times (Fuelling and Halle 2004, Krebs 2011), can have pervasive consequences for long-term fitness through reduced vital rates including survival, growth and reproduction. These may be at least as important at a population level as the fitness consequences of direct predation (Lima 1998, Heithaus et al. 2008). Consequently, the disruption of predator-prey relationships can induce trophic cascades (Paine 1980) through changes in prey population dynamics and behaviour (Berger 1999, Pace et al. 1999, Schmitz et al. 2004, Ripple and Beschta 2006). To understand the wider implications of declines in apex predator populations on communities, it is crucial to examine both their direct predatory and indirect behavioural effects on prey species (Heithaus et al. 2008).

For prey species, the mere risk of predation can influence individuals to adopt specific foraging and vigilance behaviours which reduce the threat of lethal encounters. Prey use a diversity of indirect cues to assess the level of risk of lethal encounters with predators in their environment. In the absence of direct knowledge of the whereabouts of a predator, cues such as habitat structure and time of day are used as proxies for risk (e.g. Jacob and Brown 2000,

Jones et al. 2001). Prey animals finely tune their perception of risk in their choice of where and when to forage. Proxies for predation risk include habitat attributes such as density of shrubs and ground vegetation, which can provide either better visibility or concealment from predators, and refuges for escape (Cowlshaw 1997, Jacob and Brown 2000). Animals may modify their habitat use or forage in less productive environments to reduce the risk of predation, but they must balance the cost of such behaviour against energy and fitness demands (Lima 1998, Brown et al. 1999, Brown and Kotler 2004, Lind and Cresswell 2005). For an individual, the level of investment in anti-predator behaviour may be determined by the population size and vigilance of conspecifics in addition to the predator population size (Brown, 1999).

Anti-predator behaviours can be costly to maintain, if they are energetically demanding or if they involve switching to suboptimal habitats or activity times (Lima 1998, Brown and Kotler 2004). It is clear that prey can adapt their behaviour on ecological time scales to reflect changing levels of risk (Blumstein 2002, Blumstein and Daniel 2005). If predators are lost or are absent from the environment for long periods of time, selective pressure to maintain risk-sensitive behaviours will be reduced and, given sufficient time for evolution to take place, some specific inherited anti-predator behaviours and traits may be lost (Berger 1999, Blumstein and Daniel 2005). There is evidence for heritability in some specific traits that affect predation risk, including temperament (Reale and Festa-Bianchet 2003). Some anti-predator behavioural responses have been retained in species isolated from their predators for hundreds of generations (Blumstein 2002) and are likely to be those that are not sufficiently costly to reproductive potential.

A unique opportunity to assess the effects of the progressive decline of an apex predator on prey behaviour is presented by the disease-associated decline of the Tasmanian devil (*Sarcophilus harrisii*; Marsupialia: Dasyuridae), the endemic apex mammalian predator on Australia's island state, Tasmania. Since Tasmanian devil facial tumour disease (DFTD hereafter) was first detected in the mid-1990s, the ongoing spread of this consistently fatal transmissible cancer across the geographical range of the devil has caused severe and sustained population declines (Hawkins et al. 2006, Lachish et al. 2007, McCallum et al. 2009). Once disease arrives at a site, the decline in devil populations is immediate and substantial (Lachish et al. 2007, McCallum et al. 2009). The disease has now spread to most of the devil's range, except for the north-western part of the island. It has reduced populations by about 85% overall with local declines in excess of 95%, leading to Endangered listing status with state and federal government and the IUCN. There has been no evidence of population recovery (McCallum et al. 2009) despite populations still persisting in low densities across the geographic range of DFTD.

Widespread effects on the ecosystem are expected following the decline of the Tasmanian devil, and changes in the relative abundance of smaller mammalian carnivores have already been documented (Chapter 2 and 3). Behavioural and demographic changes are also expected amongst the major prey species of devils: medium-sized macropods and possums (Jones and Barmuta 1998). These species do exhibit risk-sensitive behaviour in response to predators. Tasmania's two medium-sized macropods, the Bennett's wallaby, (*Macropus rufogriseus*), and Tasmanian pademelon, (*Thylogale billiardierii*), were shown to give up the benefits of foraging further from cover due to the perceived predation risk (While and McArthur 2006), but to emerge earlier and travel further from the forest edge in open landscapes when

predation risk was lowered (Nielsen 2009). The common brushtail possum (*Trichosurus vulpecula*) on mainland Australia, travelled further and visited more feeding patches in some habitat types in response to reduced densities of the introduced red fox (*Vulpes vulpes*) (Pickett et al. 2005). For all of these prey species, the loss of devils and the associated decline in predation risk, would likely result in an increase in activity and reduction of costly anti-predator behaviours.

The known timing and quantifiable population decline of the Tasmanian devil from DFTD provides a unique opportunity to measure changes in risk-sensitive behaviours of the common brushtail possum. In this chapter, I assess the effects of varying levels of predation risk that derive from apex predator loss on the activity and behavioural responses of the common brushtail possum. Whilst elsewhere predominantly an arboreal folivore, in Tasmania, brush-tailed possums spend considerable amounts of time grazing and browsing on the ground where they are vulnerable to predation by devils. First, I determine a relative activity index of both possums and devils by deploying hair traps in a large, rapid spatial survey in sites that have been diseased for varying lengths of time. Second, I evaluate the foraging decisions made by individual possums feeding on the ground in situations that represent different levels of predation risk from devils using a giving up density (GUD) approach based on optimal foraging theory (Brown 1988). This approach tests the decisions of the forager as it makes trade-offs between the nutritional reward gained from foraging in the patch with the costs of perceived predation risk, holding all other costs equal (Brown 1988, Brown and Kotler 2004). Differences in the GUD value, which is measured as the amount of food remaining in an artificial food patch at the end of the experimental period when the patch is surrendered, reflect the differences in the risk of predation between the patches (Brown 1988). Giving up

densities can be used to assess how foragers utilise their environment at multiple scales, which is essential to understanding the way prey species use the landscape and respond to environmental disruptions (Druce et al. 2009). I use this experimental procedure to also determine whether possums are finding food patches faster in their environment when predation risk is lower, as a measure of the extent of their ground foraging activity. Of all the potential changes that may occur with apex predator loss behavioural changes may be the most rapid and may provide an early warning and index of change.

4.4 METHODS

4.4.1 DFTD arrival times and site selection

To establish approximate estimates of the length of time that each site had been diseased, I extrapolated confirmed dates of first disease detection from surrounding regions and combined these with expected patterns of disease spread through the landscape (McCallum et al. 2007). I used the length of time since DFTD arrival at a site as a proxy for the extent of devil population decline over time, thus establishing a predation risk gradient across the island state (Figure 4.1).

I selected thirty field sites on mainland Tasmania using ArcGIS (version 9.2) based on specific vegetation and environmental attributes and representing the entire predation risk gradient. The sites chosen represented the full spectrum of DFTD arrival times (pre 1996 to still not diseased: Figure 4.1). Equal numbers of dry eucalypt forest sites and coastal woodland scrub sites were selected and matched as far as possible for the environmental variables of rainfall, elevation and temperature gradients. I conducted experiments in two different vegetation types to assess, first, if activity of prey and predator varied with habitat structure and resource availability and, second, whether attributes at a microhabitat scale affected anti-predator behavioural responses, as these variables vary between vegetation types. Common brushtail possum densities are known to vary with habitat and with disturbance (Hocking 1981, le Mar and McArthur 2005), attributed to the availability of food and shelter (Hocking 1981). Preliminary surveys showed that both habitat types supported high densities of possums. Sites were limited to the northern half of the state to avoid variation arising from any north-south environmental gradients. Specific site selection criteria were employed to

reduce the effect of culling intensity which occurs in Tasmania under crop protection permits (Driessen and Hocking 1992) and has affected the ability to monitor population trends from devil decline in a previous study (Chapter 2).

4.4.2 Index of terrestrial possum and devil activity

To obtain an activity index of devil populations and ground-based activity of possums populations across the gradient of DFTD arrival times, I conducted a snapshot survey of twenty-four of the selected sites, using equal numbers of dry eucalypt and coastal woodland scrub sites (Figure 4.1). Twenty hair tubes, consisting of a PVC pipe with double sided tape, and twenty commercially available hair funnels (Faunatech, Melbourne), were placed at each site. Half of each hair trap type were baited with carnivore bait, consisting of dried liver soaked in mutton bird oil, and half with herbivore bait, consisting of a standard universal bait of rolled oats, peanut butter and walnut oil. I placed one each of herbivore and carnivore traps, using a mixture of tubes and funnels, every 100m on alternative sides of a 2km long track. They were secured to logs or trees at ground level. In total, I deployed 960 hair traps across all sites. Samples collected from hair traps were examined from the hair medulla and cross-sectional analysis to identify species (Taylor 1985, Triggs et al. 2002). I obtained the activity index estimates from the total number of hair traps that had possum or devil hair present.

4.4.3 Giving up densities

Giving up densities have been utilised in many studies to measure the temporal and spatial use of habitat of diverse terrestrial prey species in relation to predation risk (e.g. Jacob and Brown 2000, Jones et al. 2001, Pickett et al. 2005, Druce et al. 2009, Sansom et al. 2009). I chose to use this method as it captures aggregated effect of many behaviours and foraging preferences

in a single measurable value (Brown 1988) and it reduces the risk of bias arising in observational studies, that commonly focus on a single behaviour. In experimental terms, I placed artificial food patches in environments I considered “safe”, at the base of an escape tree, and “risky”, in open ground away from any escape tree. Possums exhibit morphological adaptations for an arboreal lifestyle and would use trees to escape from predators such as devils, which are much less adept climbers. Food was mixed through an inedible matrix, and behavioural responses to changes in predation risk were measured by assessing the remaining food in each patch, termed an animal’s giving up density (Brown 1988).

To conduct the GUD experiment, I chose eighteen sites across the predation risk spectrum with equal numbers of dry eucalypt forest and coastal woodland scrub. Each site consisted of ten stations at least 100m apart on alternative sides of the track. For each station I placed a food patch at the base of an escape tree at a distance of zero meters, representing a “safe” patch and one food patch between five and twelve meters from the base of any escape tree in open ground representing the “risky” patch. “Risky” patches were as far as possible from an escape tree, but the distance was limited by the proximity of neighbouring escape trees. I defined an escape tree as having a minimum of 10cm in diameter at breast height (Pickett et al. 2005), selecting trees which had evidence of possum use, such as scats on the ground or scratching in the bark, wherever possible. The distance to the nearest escape tree measured the potential “safety” or “riskiness” of the food patch.

The food patch comprised a 4L round container filled with 2.5L of medium-sized river pebbles as the non-edible substrate, with 100 sultanas (dried grapes) mixed through the pebbles. The container had a lid with a 10cm diameter hole cut into it, allowing either a head or a paw into the container but not both, thereby affecting foraging capability. Possums were

able to sort through the substrate for sultanas but the design inhibited their ability to empty the container of rocks and therefore food. Sultanas were chosen as the reward as they are easy to identify and do not break down when wet as do many commercially available pellets. They were also shown to be a highly attractive food source for common brushtail possums in a similar study on mainland Australia (Pickett et al. 2005). I considered counting the sultanas to be the most accurate method, as dirt and moisture could affect the weight, giving misleading results, particularly in variable weather conditions that are typical of the temperate Tasmanian climate. I deployed the feeding patches for a total of four nights and they were checked every morning during this period. If there was evidence of visitation, I counted the remaining sultanas and restored the food patch with 100 fresh sultanas. Once feeding patches were found by possums, they were invariably visited on subsequent nights.

Foraging by non-target species was limited by the design of the containers and substrate. Rarely did non-target species take more than 15% of the food and never more than 25%. The weight of the substrate and space within the container reduced small mammal activity and the lid prevented wallaby foraging, as observed from motion activated camera footage and assessed during an initial pilot study on feeding patch design. To determine the species responsible for foraging in the food patch on a particular night I recorded activity using motion-activated cameras, or alternatively, double sided tape was placed around the edge of the container and the hair identified. Where there was evidence of non-target species and no possum activity, data were discarded.

I conducted habitat surveys at each food patch to assess whether microhabitat variables were important predictors of an individual's anti-predator behaviour response. Microhabitat has been documented in previous studies to affect prey foraging behaviour in the presence of

predators (e.g. Lima 1998, Pickett et al. 2005, Druce et al. 2009). Microhabitat variables which could influence foraging behaviour and predator detection of possums were estimated at each food patch. These were the percentage of open ground cover, measured as cover below 50cm; percentage shrub cover, as measured from 50cm to 2m; and the percentage of tree canopy cover in a 5 meter radius.

4.4.4 Statistical analysis

Activity patterns of possums

To assess apex predator effects on the activity patterns of possums I fitted generalized linear models (GLMs) to the data for the number of hair-traps that trapped possum fur for each site using R (R Development Core Team 2011, version 2.11.0). GLMs assume linear relationships between combinations of predictors and the link function. I used them to determine whether the activity of devils, as a measure of predation pressure during the study season, and the year since DFTD arrival, as a predictor of devil populations and predation risk through time, were important factors in possum activity. Vegetation type was also incorporated into models as a categorical variable of either dry eucalypt forest or coastal woodland scrub. All combinations of predictor variables were modelled, giving a total of eight models in the candidate model set including the null model. I applied a negative binomial error structure with log link function to account for overdispersion in the data. To assess the support for alternative models I used the weights (w_i) derived from small sample corrected Akaike Information Criteria (AICc), where the weight provides the relative support for each model (Burnham and Anderson 2002).

Time taken to find food patches

I applied survival analysis, using a Cox proportional hazards model, to data on the time taken for possums to find individual feeding patches across the varying predation risk gradient.

Survival analysis is used for analysing data where the dependent variable measures the time to the occurrence of an event and where the occurrence of the event may not occur for all subjects (Hosmer et al. 2008). The data was right censored as not all of the food patches were found by possums when the experiment was terminated after four nights. For each night at each individual food patch, I recorded a “0” if the patch had not been found and a “1” on the first night of the experiment that it was found and foraged by a possum, indicating the end of the event. If a patch had not been found and was still scored “0” on the fourth night, the data for that patch was considered to be censored. For visualisation purposes, I divided the sites into three DFTD arrival regions of early disease, mid-term disease and disease free (See Figure 4.1) and drew a Kaplan-Meier product-limit graph which estimates the survival function, of the feeding patch not being found, against time (Crawley 2007, Hosmer et al. 2008). For the regression model, I used a continuous variable of years since DFTD arrival as the measure of predation risk, in addition to the three microhabitat variables as for the GUDs analysis. The best model was chosen using AICc weights as in previous analyses.

Giving up densities analysis

I used generalized linear mixed models (GLMMs) to assess the anti-predator behaviour of possums from their giving up densities (using the lme4 library in R version 2.11.0) with Gaussian error structure and identity link function. These models included random effects in the linear predictor to account for pseudo-replication in the study design of firstly, multiple

stations for each site and secondly, the multiple nights surveyed at each individual feeding patch. The relationship between the total amount of food remaining in a feeding patch, representing an individual's giving up density, was modelled against several predictor variables: the estimated predation risk quantified as the number of years a site had been diseased; the three microhabitat variables; the vegetation type; and the measure of riskiness of the feeding patch represented by the distance to an escape tree measured in metres. Distance to escape tree was modelled as an interaction term with both years diseased and vegetation type because the importance of distance to safety for possums may vary with the local devil population and the availability of escape trees which differs with vegetation type. All combinations of predictor variables including interaction terms were modelled and the null model. Correlation between variables was assessed prior to inclusion in the model, using Pearsons correlation coefficient.

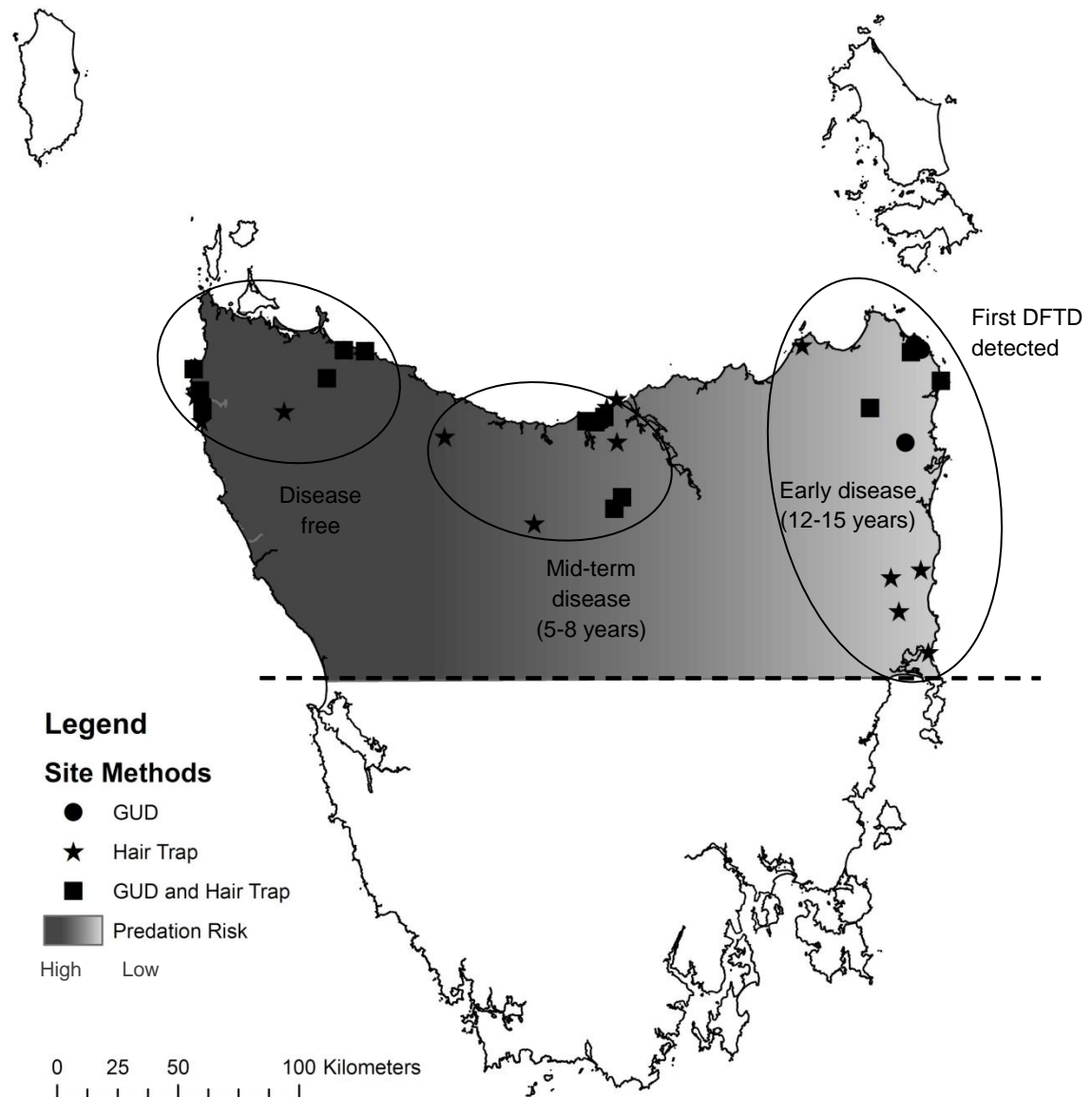


FIGURE 4.1: Field site locations for GUD experiment and hair traps. Circles enclose the sites for the three predation risk regions of low (early disease), medium (mid-term disease) and high (disease free). Sites are limited to the northern half of the island state. Predation risk represents the projected level of predation as interpolated from DFTD arrival times and corresponding devil decline.

4.5 RESULTS

4.5.1 Terrestrial possum and devil activity

The effects of DFTD on devil populations are extensive (Figure 4.2) with most sites having low or no hair trap hits when DFTD has been present for more than 8 years. This corresponds well with previous evidence of severe and significant declines within just a few years subsequent to DFTD arrival (Lachish et al. 2007, McCallum et al. 2009, Chapter 2). Possum activity varies considerably between sites and possums maintain populations in all areas of the state even in the presence of high devil populations (Figure 4.2). The number of positive hair traps indicates that there is a significantly higher ground-based possum activity with increasing number of years since DFTD arrival and subsequent devil decline (parameter estimate = 0.04 ± 0.02 SE, $p < 0.05$) and a corresponding negative relationship with the activity of devils (parameter estimate = -0.07 ± 0.04 SE, $p < 0.05$). The model containing both these variables ranked highest, carrying 41% of the weight in the candidate model set (Table 4.1). The second and third ranked models contained single co-variables of the length of time diseased and devil activity respectively. The vegetation type did not play an important role in the activity of possums and the model containing this single co-variate had a higher AICc value than the simple null model.

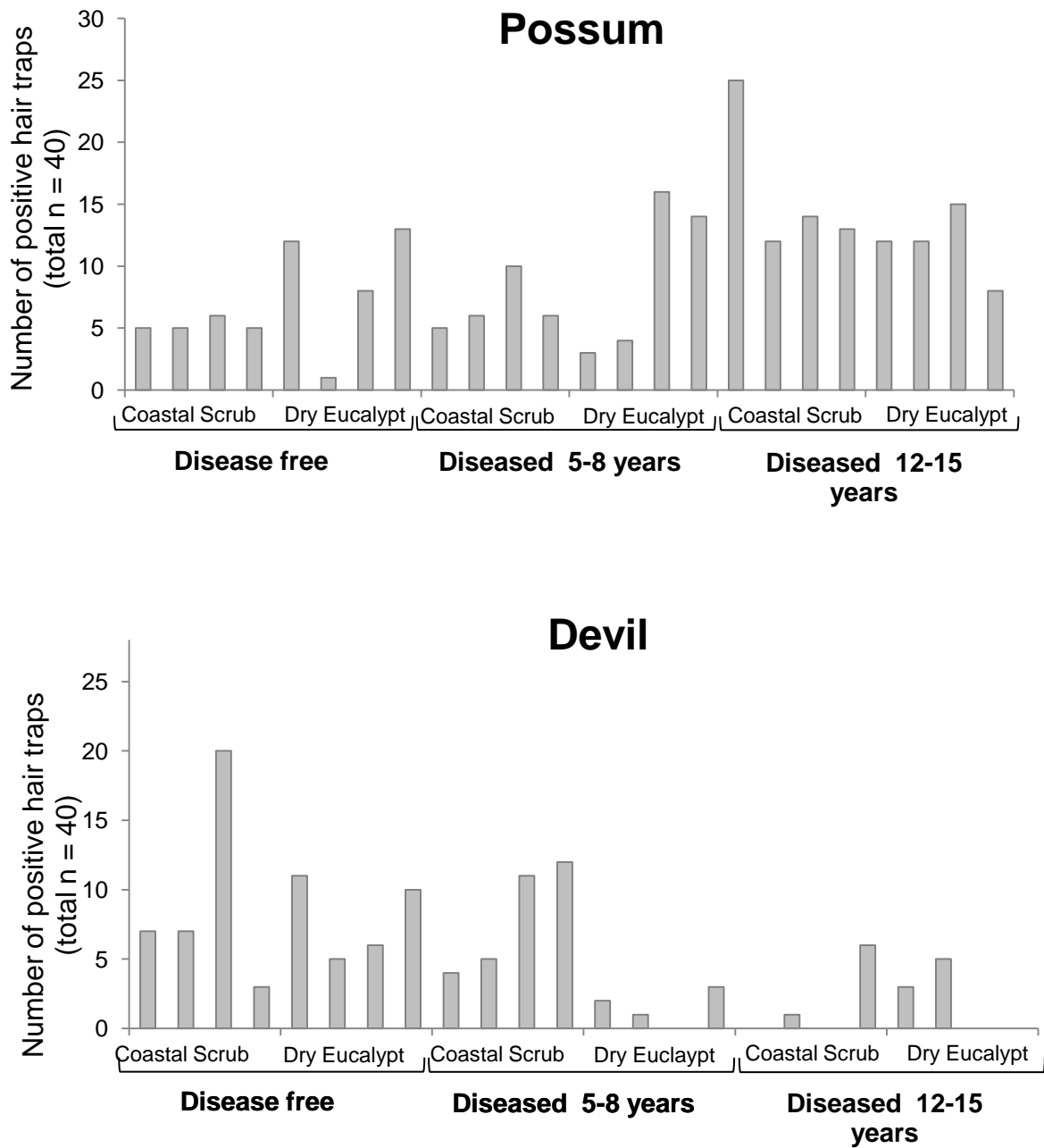


FIGURE 4.2: Number of hits of hair traps by devils and possums as an index measure of activity in dry eucalypt forest and coastal woodland scrub habitat types across sites with a range of DFTD arrival times.

TABLE 4.1: *The best supported models from the GLM analysis assessing factors affecting the activity index of possums measured through hair-trap hit rates*

Model parameters	Model rank	k	$\Delta AICc$	w_i
Years diseased + devil abundance	1	4	0.00	0.41
Years diseased	2	3	1.25	0.25
Devil abundance	3	3	2.22	0.15
Null	7	2	4.87	0.00

4.5.2 Time to find food patches

Possums found feeding patches much sooner in areas of lower devil densities (Figure 4.3), with years since DFTD arrival significantly and positively associated with the time it took for this to occur (Table 4.2). The estimated Hazard Ratios (Table 4.3) indicated that for every year since DFTD arrival there was a 4.5% increased chance of a feeding patch being found. After a site has been diseased for more than five years, this equates to a 25% increased chance of finding the feeding patches ($1.25 = \exp(5 \times 0.045)$). Possums discovered food patches earlier in areas with a higher proportion of open ground cover, and in coastal woodland scrub. For a 1% increase in the proportion of open ground cover, there was a 1.6% increase in the chance of a feeding patch being found (Table 4.3). There was some evidence to suggest that tree canopy cover and shrub cover, which affect visibility of prey from above by avian predators, may have influenced whether possums found food patches. The weight of the

models containing these variables, which indicates the relative importance of the variables, was 55% and 33% respectively (Table 4.2).

TABLE 4.2: *The set of Cox proportional hazards models within a $\Delta AICc$ of 2.0 for the number of nights for a possum to find food patches across a predation risk gradient. The table shows the model rank, the change in $AICc$ ($\Delta AICc$) from the top model, model weights (w_i) and model coefficient estimates $\pm 1SE$ for each explanatory variable. An * indicates $p < 0.05$, ** indicates $p < 0.01$. The relative importance of the variable denotes the sum of weights of all candidate models containing the variable, despite not all models being shown here.*

Survival Analysis							
Model Rank	$\Delta AICc$	w_i	Model Explanatory Variables				
			Vegetation type (Dry)	Open ground cover	Years since DFTD arrival	Tree canopy cover 5m	Shrub cover
1	0.00	0.27	-0.310 \pm 0.127*	0.015 \pm 0.003**	0.044 \pm 0.010**	0.003 \pm 0.002	
2	0.25	0.24	-0.325 \pm 0.126*	0.015 \pm 0.003**	0.041 \pm 0.010**		
3	1.75	0.11	-0.316 \pm 0.127*	0.016 \pm 0.004**	0.044 \pm 0.010**		0.002 \pm 0.003
4	1.81	0.11	-0.304 \pm 0.127*	0.015 \pm 0.004**	0.045 \pm 0.010**	0.003 \pm 0.002	0.002 \pm 0.003
Null	42	0.00					
Relative importance of variable			92	100	100	55	33

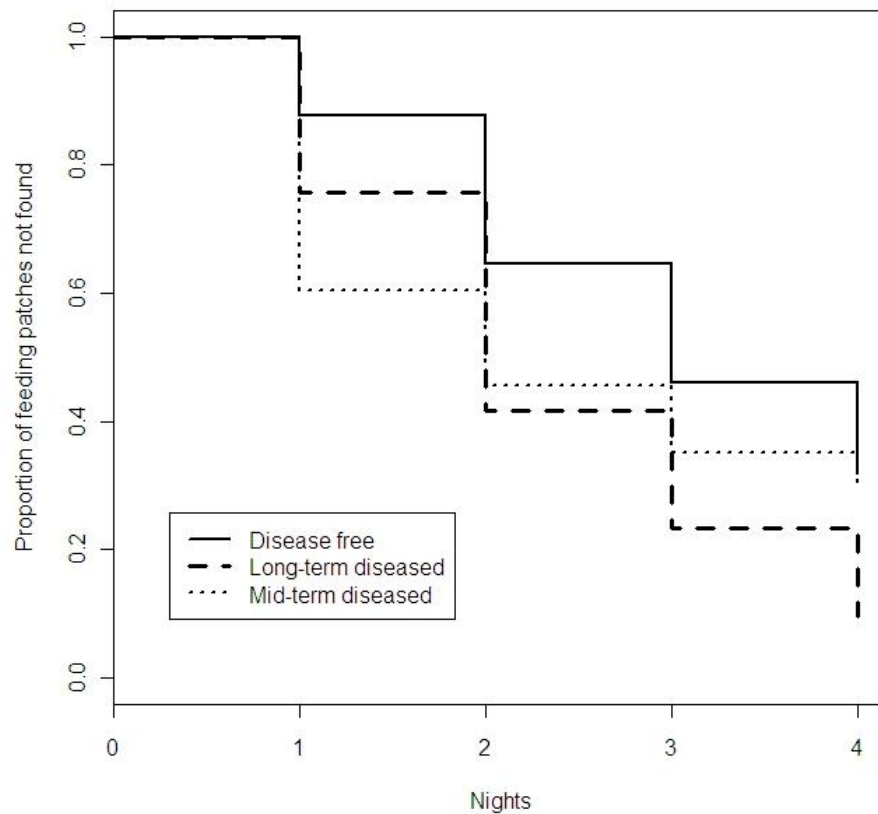


FIGURE 4.3: *Kaplan-Meier estimates of the survival function for the proportion of feeding patches not found by possums over the four nights they were deployed.*

4.5.3 Giving up densities

The most parsimonious model explaining the amount of food remaining in artificial food patches included four variables: percentage of open ground cover, distance to escape tree, years diseased and vegetation type. There were two interaction terms: the year since DFTD arrival with distance to escape tree and the vegetation type with distance to escape tree (Table 4.4). This model received overwhelming support with 82% of the weight in the candidate model set. The inclusion of these interaction terms in the model suggests that the distance

from escape tree becomes less important as the number of years since DFTD arrival increases. This was highly significant (interaction term: est, = -0.10 ± 0.03 SE, $p < 0.001$) and distance from escape tree was also significantly more important in coastal woodland scrub than in dry eucalypt forest (interaction term: est = -1.22 ± 0.39 SE, $p < 0.002$). In addition, the more open the ground cover surrounding a food patch the lower the giving up densities (est. = -0.21 ± 0.07 SE, $p < 0.005$), suggesting that possums perceive feeding patches in open ground to be safer and have a lower cost. Shrub cover and tree canopy cover did not play a significant role in explaining the GUDs for possums.

TABLE 4.3: *Estimated Hazards Ratios and 95% Confidence Interval Estimates for variables in the best supported Cox proportional hazard model of the time until feeding patches were found across the predation risk gradient.*

Variable	Hazard ratio	95% CI
Vegetation type	0.729	0.569,0.935
Open ground cover	1.016	1.009,1.023
Years since DFTD arrival	1.045	1.024,1.066
Tree canopy cover (5m)	1.003	0.996,1.009

TABLE 4.4: *Most parsimonious GLMM model with explanatory variables for giving up densities and model parameter estimates explaining the importance of factors in possum anti-predator behaviour. The response variable is the number of sultanas remaining in a feeding patch.*

GLMM models				
Parameters	Model rank	k	ΔAIC_c	w_i
Open ground cover +Dist escape tree:Years diseased + Dist escape tree:Vege type	1	10	0.00	0.82
Open ground cover + Dist escape tree:Years diseased + Vege type	2	9	4.69	0.08
Open ground cover +Dist escape tree:Years diseased + Dist escape tree:Vege type + Shrub cover	3	11	6.42	0.03
Open ground cover +Dist escape tree:Years diseased + Dist escape tree:Vege type + Tree canopy cover	4	11	7.16	0.02
Open ground cover +Dist escape tree + Years diseased	5	7	7.46	0.02
Null model	21	4	21.12	0.00
Parameter estimates for top model in candidate model set				
Parameter	Estimate		SE	
Intercept	60.95		6.09	
Open ground cover	-0.12		0.05	
Dist escape tree	1.87		0.40	
Years diseased	-0.85		0.40	
Vege type (Dry)	-3.21		5.20	
Dist escape tree:Years diseased	-0.09		0.03	
Dist escape tree:Vege type (Dry)	-1.04		0.40	

4.6 DISCUSSION

The common brushtail possum is altering its foraging behaviour in a direct and dynamic response to the recent and ongoing decline of a major apex predator by increasing the extent of their terrestrial activity and foraging further from spatial refuge. The higher possum activity levels I recorded using the hair traps and earlier discovery of artificial food patches in regions with lower devil density may represent early evidence for prey release if behavioural changes translate into increased fitness over time. The lower giving up densities in food patches further from refuge reflects favourable trade-offs between harvest rate and reduced predation risk.

When foraging on the ground, possums are highly sensitive to microhabitat variables, such as open vegetative ground cover, which allow early detection of ground-dwelling predators and this relationship is seen irrespective of the level of predation risk from devils. Given the very recent decline of devils in the landscape, the findings suggest that relaxation of some risk-sensitive behaviours by possums may occur rapidly and potentially result in positive demographic responses.

The higher terrestrial activity of possums in areas with lower predation risk, as seen in both the hair trap surveys and the earlier detection of artificial food patches, may be a function of an increase in ground-foraging behaviour, changes in habitat use, greater population abundance, or combinations of all three. Over longer timeframes, behavioural adaptations which can occur immediately, have been linked to fitness and reproductive potential and could conceivably be linked with prey release and increasing abundance (Morris et al. 2009). Lethal effects of predation can often mask the nonlethal effects associated with the mere presence of predators in an ecosystem (Lima 1998). These indirect effects may have a stronger influence on food web dynamics by manipulating behaviour and regulating populations. There is no

definitive evidence for how behaviourally mediated changes to an individual's predator response affect their fitness (Lima 1998, Lind and Cresswell 2005). One measure of fitness, reproductive rates, can be reduced by the perceived risk of predation (Fuelling and Halle 2004, Krebs 2011), which could in turn reduce prey population size. The influence here is that following apex predator loss, the combined effects on fitness of decreased lethal interactions and the reduced costs associated with anti-predator behaviours, means energy can be reinvested into reproductive potential and fitness.

The giving up densities demonstrates that possums are changing their anti-predator behaviours irrespective of any changes to population size or density. For many vertebrates, the physical characteristics of their environment significantly affect their perceived level of risk and they will modify their use of space accordingly (Lima 1998, Jones and Dayan 2000, Druce et al. 2009). The significant interaction between foraging distance to an escape tree and time since DFTD arrival shows that once predation risk from devils is reduced to a low level, possums are much less sensitive to the distance at which they will forage from spatial refuge. In areas of lower devil densities, the lower giving up densities indicates that the importance of distance to a tree, which allows possums to escape from terrestrial predators like the devil, is diminished. The percentage of open ground cover was significantly important to the giving up density of possums in areas of high devil abundance. This contrasts with many terrestrial prey species which have higher giving up densities in open habitats (e.g. Brown and Kotler 2004). Shrubs, however, can hamper the detection of predators for many larger terrestrial mammals by affecting their ability to monitor the landscape (Druce et al. 2009).

The importance of both distance to escape tree and open ground cover as anti predator behaviours is consistent with what is known of devil hunting behaviour. Tasmanian devils are

believed to be pounce pursuit predators, with a preference to hunt in open habitats (Jones and Stoddart 1998). The preference for possums to forage in open ground may reflect a strategy of early detection of terrestrial predator species, having the advantage of an arboreal escape strategy and impeding the ability of predators to conceal themselves on approach. This may also explain the variation in importance of distance to escape tree in different habitat types, where dry eucalypt forest, with a more complex habitat structure, may offer multiple modes of escape. These findings may represent a reduction in risk sensitive behaviours that relate specifically to devils, while possums are maintaining vigilant behaviours appropriate for alternative predator species (Berger 1999). It may also represent selection against behaviours that limit possums foraging in the most optimal and rewarding habitats.

Microhabitat variables that affected possum foraging behaviour suggest that the mode of predation may contribute to the patch specific predation risk to possums. Some anti-predator behaviours expressed by possums appear to be species-specific to devils, and others may be directed towards alternative terrestrial and possibly avian predators which was reflected in the importance of tree canopy and shrub cover in the time taken to find feeding patches. Different predator species, and their hunting styles may elicit specific behavioural responses in prey (Schmitz and Suttle 2001). The smaller terrestrial predator species and ambush style hunters, the native spotted-tail quoll (Jones and Stoddart 1998) and the feral cat, are also known to consume brushtail possums (Belcher 1995, Molsher et al. 1999, Dawson et al. 2007). The distance to perceived safety, measured as an escape tree, may be important for avoidance of devils, but would be less effective against these species which have the capacity to climb and are both partially arboreal. Following the competitive release of cats (Chapter 2 and 3) and potentially other predators following devil decline in some areas, anti-predator behaviours

specific to these mesopredators may be observed more frequently in these areas. There is also a low density and breeding population of foxes in Tasmania (Saunders et al. 2006, Sarre et al. 2012), which have been shown to induce vigilance behaviours in common brushtail possums on mainland Australia (Pickett et al. 2005). They have not yet become established in Tasmania and their effects are unknown.

Risk-sensitive foraging behaviours vary between species, even in response to the same predator (Schmitz et al. 2004). This reflects the biology of the prey species. Possums, as partially arboreal and solitary, will employ different vigilant behaviours to predators than wallabies, which are ground dwelling and live in loose social groups. Prey will exhibit behaviours which are a functional response to their specific vulnerabilities and strengths. This makes it difficult to extrapolate effects associated with apex predator decline across a broad range of prey species. In addition, complex environmental variables can affect population trends and behaviour of prey species irrespective of apex predator decline. Lower than average rainfall for example may increase the distance individuals need to forage from safety (Driessen and Hocking 1992).

This study provides evidence for both increasing possum activity which may be a function of prey release, and definitive variation to behaviour correlated with devil density, and suggests that an element of top-down control exists for the common brushtail possum in Tasmania.

Any positive changes to the population dynamics and behaviour of herbivore prey species from the disruption of predator-prey relationships has the potential to initiate a trophic cascade (Paine 1980, Berger 1999, Pace et al. 1999, Schmitz et al. 2004). Should possum abundance increase as a result of reduced predation from devils and relaxation in potentially costly anti-predator behaviours, there may be trophic cascade effects due to possums being both browsers

and grazers. Evidence of trophic cascades has been demonstrated in all major biomes on earth (Estes et al. 2011) and has been supported by a significant number of studies assessing the loss of apex predators (e.g. Terborgh et al. 2001) and retrospectively with the reintroduction of apex predators into their former range (e.g. Ripple and Beschta 2007, Berger et al. 2008).

Reintroduction of apex predators into ecosystems may be one way to re-establish predator prey interactions and limit the magnitude of trophic cascades. This has been observed following the reintroduction of gray wolves (*Canis lupus*) into Yellowstone Park in North America in the mid-1990's which resulted in both behavioural and density changes of herbivore populations, leading to reduced grazing pressures (Laundre et al. 2001, Ripple and Beschta 2007). It can however be difficult to distinguish between density and behaviour-related effects of browsers and grazers and the evidence for behaviourally mediated trophic cascades remains controversial (Creel and Christianson 2009, Kauffman et al. 2010). Any behavioural or demographic response of prey species to the loss of predators may invoke cascading effects through lower levels of the food web and modification of plant communities (e.g. Terborgh et al. 2001, Ripple and Beschta 2008) as they utilise a greater range of habitats which may offer greater energetic returns. Unfortunately, due to the nature of DFTD and its ability to persist in low density populations (Hamede et al. 2008, McCallum et al. 2009), reintroduction is unlikely to be a viable option for Tasmanian devils prior to extinction of wild populations. The widespread and substantial culling of common brushtail possums and other native herbivores, which has been in place for decades, is likely to limit the scale and extent of any measurable trophic cascades in Tasmania initiated by devil decline and potential corresponding increases in herbivores.

The extensive and continued loss of apex predators from environments worldwide is having far-reaching effects, linking all levels of a food-web in often complex and unexpected ways. The importance of prey behaviour may be under-appreciated as a major influence and driver of ecological systems and a change in this behaviour may be amongst the most rapid responses to such a decline. In ecology the top-down regulation of ecosystems, from indirect effects cascading through lower levels of the food web, are some of the strongest indirect effects to have ever been revealed (Lima 1998). The implications of predation and predation risk on the structure and function of food webs remains largely speculative (Schmitz et al. 1997). The extent of the loss of anti-predator behaviours and species interactions following any decline in large carnivores should be addressed to determine whether prolonged periods of apex predator loss may compromise prey behaviour and interactions (Berger 1999) to the detriment of ecosystem dynamics and stability.

4.7 ACKNOWLEDGEMENTS

I would like to acknowledge my funding body, the Save the Tasmanian Devil Appeal through an Eric Guiler Tasmanian Devil Research Grant, for funding this research. I would also like to extend my sincere thanks to the volunteers who assisted me with the hours of monotonous sultana counting, even in extreme weather conditions that such a project entailed.

This chapter has been removed for
copyright or proprietary reasons.

Chapter 5

Wildlife disease ecology in changing landscapes: mesopredator release and toxoplasmosis

Published In:

<http://www.sciencedirect.com/science/article/pii/S2213224413000035>

Hollings, T., Jones, M., Mooney, N., McCallum, H. 2013 Wildlife disease ecology in changing landscapes: mesopredator release and toxoplasmosis. *International Journal for Parasitology: Parasites and Wildlife*. Vol. 2, pp. 110-118.

Chapter 6:

General

Discussion



6.1 Introduction

The disease-induced decline of Tasmanian devils, although poignant, provides a unique, natural and large-scale system in which to study the ecological effects of the loss of an apex predator and keystone species. Rarely do studies of mammalian apex predator loss provide the opportunity to assess the extent of changes in lower trophic levels in known timeframes, or have the benefit of large spatial gradients of declining predator densities. The aim of this thesis is to determine the overarching effects of the loss of an ecologically functional devil population on the terrestrial mammalian fauna of Tasmania. The research questions represent some of the major ecological disruptions related to mesopredator release, behaviour and community composition that are expected following apex predator loss and are formulated from community ecology theories.

In this section, I synthesise the findings of this study and examine whether there is evidence for the patterns observed, and their underlying processes, to represent consistent and widespread effects of global apex predator loss. In light of the success of recent reintroduction of apex carnivores, I consider the potential for the restoration of top-down control from both the Tasmanian perspective and globally. I examine the challenges faced by large scale apex carnivore studies and outline promising future directions for multidisciplinary research. The results of this research provide a novel contribution to the study of apex predator loss and enhance our current understanding of the capacity of apex predators to shape ecosystem structure and function.

6.2 The ecological effects of DFTD and their significance for global apex predator loss

Due to the sustained and severe declines in devil populations occurring over a very short timescale there is an urgent need to measure and understand the consequences of devil decline, so that mitigating actions can be taken. One of the three major objectives of the Tasmanian State Governments Save the Tasmanian Devil Program (STTD) is to “manage the ecological impacts of a reduced Tasmanian devil population over its natural range” (STTD, Strategic plan). This objective is currently in the phase of determining what effects are likely to occur before actions can be implemented to mitigate some of those effects. My study represents the first quantitative research on the ecosystem effects of devil population decline and therefore one of the first steps towards realising the STTD objective. My results provide information critical to guiding the effective design and implementation of management actions

Consequences of devil decline: summary of key findings

- Feral cat numbers generally increased, consistent with mesopredator release theory
- Increasing feral cat populations placed increased pressure on native species, including the eastern quoll and rodents
- Invasive species at all trophic levels generally increased in response to devil decline, in contrast to native species,
- In areas of long-term devil decline species diversity reduced, leading to homogeneous communities and a higher proportion of invasive species
- Prey species of devils reduced vigilant behaviours that are specific to the risk of predation by devils and increased activity in response to devil decline. This occurs on a relatively short timescale
- The level of *Toxoplasma* infection in wildlife was higher in regions with higher cat density, suggesting that devil decline may indirectly lead to increased *Toxoplasma* transmission.

to alleviate any adverse ecological effects. The loss of Tasmanian devils from DFTD over large tracts of Tasmania is cause for concern not only for the long-term viability of devil populations, but also for the persistence of other species and the maintenance of biodiversity. This is particularly pertinent on an island where healthy populations of many species now extinct or endangered on mainland Australia have survived (Recher and Lim 1990).

Ecosystem effects of devil decline may take years or decades to manifest. To overcome this limitation, and to provide useful information on the time frame of a three-year PhD, I combined a range of approaches. Taken individually each approach has its shortcomings. For example, the spotlighting data, whilst it is a longitudinal dataset, was collected for a different purpose and contains some measurement error. This limits the extent to which clear signals can be derived from this particular data set. In contrast, the chapters on the spatial analysis of mesopredator and prey, anti-predator behaviour and disease ecology (Chapters 3, 4, 5) were designed explicitly to examine the consequences of devil decline but substitute space for time. Data for these three chapters were collected over a short time period and cover a broad geographic area, encompassing differing devil densities. The large geographic extent of sampling means that variables other than devil density differ among the sites, despite attempts being made to match the sites for environmental variables such as vegetation and rainfall. Despite some limitations, taken together these differing approaches produce consistent results. Following devil decline, feral cat occurrence (and consequently *Toxoplasma* prevalence) has increased; herbivore relative abundance has increased and their foraging has become less risk-averse; and there is evidence of a second order effect of decline in eastern quolls and native small mammals. That there are consistent broad-scale changes observed using a range of approaches and methodologies provides confidence that real changes in the ecosystem have

been detected as a consequence of devil decline. The overall conclusions of the study are thus stronger than the sum of its parts.

The combined empirical evidence from this study corresponds well with effects reported internationally across a diverse array of ecosystems. The consistent patterns revealed irrespective of the specific ecosystem or species assemblages indicate that lessons learnt from Tasmanian devil decline could be globally significant and applicable in other ecosystems. For example, the importance of geographic variation in environmental and anthropogenic variables in driving patterns, particularly the relative strength of bottom-up regulation, was highlighted. These factors could impede the generalisation of effects across the entire geographic range of a species. In addition, invasive system states and the responses of species of different origins are less extensively studied but could be important drivers of changes in community dynamics and biodiversity composition. My results highlight the contrasting responses of similar-sized native and introduced species to changing pressures, with introduced species responding favourably to ecological disruption. This finding may not necessarily be context dependent, as successful invaders share common attributes (Boitani 2001). The changes in disease dynamics in relation to mesopredator release found in this study represent a step towards more wide-ranging studies that are currently outside the scope of most research into apex predator loss. Large-scale natural experiments such as this are an invaluable resource to assess and predict common trends associated with apex predator decline.

6.3 Does the loss of apex predators lead to increasingly invasive states, declining ecosystem complexity and reduced resilience of biodiversity?

Similar patterns of the effects of apex predator loss on community structure and biodiversity are emerging from a variety of ecosystems. The culmination of empirical evidence from ecosystems indicates that the presence of apex predators provides a buffer to biodiversity loss. Any population declines at top trophic levels may have cascading effects to lower levels of the food web, and could affect the persistence of many species. Beyond food webs, apex predator loss can influence ecosystem process such as fire regimes, carbon uptake, and interrelationship among soil, water and the atmosphere (Estes et al. 2011). My results show that the Tasmanian ecosystem is responding in a fashion similar to a wide array of ecosystems internationally. Here, I found evidence of higher proportions of invasive species, lower native fauna diversity and more taxonomically restricted community composition in areas of severe and long-term apex predator suppression.

World-wide declines in populations of apex predators have lead to simplified ecosystems (e.g. Terborgh et al. 1999, Estes et al. 2011) and increasingly invasive states (Wallach et al. 2010). Invasive carnivores can have damaging effects on their new environments. Nearly half of all successful introduced species have reduced the densities of native prey species (Boitani 2001). I found support for mesopredator release of feral cats from the combination of two studies covering extensive spatial and temporal scales (Chapter 2 and 3). In both approaches, environmental variables and anthropogenic influences determined the strength of the top-down effect. Invasive predators, such as feral cats, have the capacity to drive community structure (Croll et al. 2005) and are more detrimental to indigenous prey than native predators (Salo et al. 2007). Feral cats predate on small and medium-sized vertebrates and it is probable

that their release from competition from devils in Tasmania is increasing predation pressure on native species. The observed concomitant decline in eastern quolls and native rodent species support this hypothesis.

Successful introduced carnivores share common characteristics, such as medium body size, wide prey range, high fecundity and they are often habitat generalists (Boitani 2001). Both feral cats and red foxes share these traits. Following their introduction into Australia, they have been linked with population declines of native marsupials and appear to benefit from apex predator loss (Smith and Quin 1996, Glen and Dickman 2005, Johnson et al. 2007, Letnic et al. 2009b). This study provides some evidence that the devil, in a similar way to the dingo (Dickman 1996, Johnson et al. 2007, Letnic et al. 2010), limits feral cat populations and provides protection for native biodiversity. High densities of devils may have also acted as a barrier in preventing fox establishment in this and in previous incursions, probably due to competition for food and den sites and predation of fox litters (Bloomfield et al. 2005). Whilst the research for this thesis does not include foxes, they are of significant conservation concern in the Tasmanian environment. There are 78 native terrestrial vertebrate species that would be at risk from fox predation in Tasmania and some of these are considered threatened or have restricted ranges (Saunders et al. 2006). A significant proportion of these species are within the prey size range of other larger mesopredators and may not exhibit appropriate anti-predator behaviours towards new threats. For example, eastern quolls and native rodents are naive to cues of novel introduced predators, and do not respond as they do for native predator cues (Jones et al. 2004b, McEvoy et al. 2008). The defences of native biodiversity may be a key determinant of their long-term survival.

Species origin can influence their response to environmental perturbations. In this way, changing environmental conditions that favour invasive species may allow them to dominate over native species, which might be constrained by the same processes (MacDougall and Turkington 2005). In this study, invasive species at all trophic levels responded positively to apex predator loss and human modified landscapes, in contrast to ecologically similar native species which responded negatively. For example the native spotted-tailed quoll, which has a similar body size and prey range to feral cats, occurred at highest densities at medium levels of devil decline and lowest densities in areas of long-term devil decline, which incidentally exhibited the highest levels of cats. This could arise from naïveté to threats from introduced species (McEvoy et al. 2008) or the ability of these species to outcompete native species for shared resources. This differential response in introduced and native species may signify a shift towards a more invasive dominated mammalian community in Tasmania. This is further supported by significantly greater proportions of invasive species in areas of long-term devil decline. My results provide empirical support for the hypothesis that global apex predator loss leads to more invasive and homogenised communities, which is increasing threats to ecosystem resilience and persistence of native biodiversity.

6.4 Do environmental factors and predator guild dynamics influence the strength of interactions and the magnitude of responses to apex predator loss?

The role of top-down and bottom-up regulation is an issue of contention among many ecological researchers and arises from the complex nature of species relationships (Terborgh et al. 1999). Despite the strong evidence for mesopredator release, environmental variables and bottom-up processes also exert strong regulating forces on populations. For example,

agricultural expansion and associated habitat fragmentation may favour populations of red foxes (Litvaitis and Villafuerte 1996, Elmhagen and Rushton 2007) and urbanisation can influence the community structure and population demographics of mesopredators (Prange and Gehrt 2004). While the removal of top-down control leads to increasing mesopredator populations, the magnitude of any population increase may be determined by bottom-up processes and the productivity of the ecosystem (Elmhagen and Rushton 2007). My results, compiled from a large temporal and spatial extent across environmental gradients, correspond well with these global patterns. In Tasmania, agricultural landscapes favour the bottom-up regulation of mesopredators, while in less disturbed regions top-down control is the principal regulating force. This indicates that environmental variables are having a strong influence on the strength of interactions between trophic levels in the Tasmanian ecosystem. This may be true for the large majority of ecosystems worldwide where apex predator density and ecosystem productivity both determine the extent to which mesopredator and prey populations are controlled via top-down and bottom-up processes (Elmhagen and Rushton 2007, Elmhagen et al. 2010).

For all ecosystems, it is probably that both top-down and bottom-up regulation act simultaneously (Terborgh et al. 1999). Large-scale studies of the ecological effects of apex predator loss are rare (Estes et al. 2011), and may not include important environmental variables which influence the strength of species interactions. The results presented here highlight the importance of large-scale and multifaceted studies that account for bottom-up regulatory processes, to fully appreciate the strength of apex predator relationships with lower trophic levels.

Complex interactions and diversity in food webs, particularly at intermediate trophic levels, can dampen the strength of trophic cascades (Pace et al. 1999, Schmitz et al. 2000). The magnitude of top-down control and trophic cascades can be diminished where there is high intra-guild predator diversity (Finke and Denno 2004). Intraguild predation, whereby one predator species consumes another with which it directly competes (Polis and Holt 1992), and behavioural changes in response to larger carnivores may both play a role in reducing the strength of trophic cascades. The unique and complex guild of higher order carnivores in Tasmania makes predicting the nature of predator guild relationships challenging. Studies on interactions between native carnivore species in this system have shown strong evidence for competition on ecological (aggressive competition and diet overlap) and evolutionary (character displacement) scales (Jones 1997, Jones and Barmuta 1998). Despite this, there is no definitive evidence for intraguild predation in this system either among native species, or with the addition of the invasive feral cat. A decline in eastern quolls was observed corresponding with an increase in feral cat occurrence. This may represent indirect evidence for predation and competitive suppression, however despite the strong relationship, the evidence remains correlative rather than causal. The two native mesopredators also expressed variation in activity times across different DFTD arrival regions. The evidence from this study suggests that complex and multifaceted relationships exist among species within the predator guild. These complex interspecific interactions will influence the magnitude of ecosystem effects attributable to apex predator loss. Increased intraguild predation and behavioural suppression can reduce pressure on prey populations (Polis and Holt 1992, Vance-Chalcraft et al. 2007).

Top-down control is generally assumed to occur through lethal interactions, however much of the top-down control exerted by apex predators may be transmitted through behavioural changes (Lima 1998). Although less apparent, indirect effects of predators may have a stronger influence on food web dynamics than direct predation events (Beckerman et al. 1997, Schmitz et al. 1997, Lima 1998). For species at lower trophic levels, competitive interactions and the mere risk of predation can influence individuals to adopt specific foraging and vigilance behaviours to reduce the threat of lethal encounters. The intensity of nonlethal interactions may vary for specific individuals, species and trophic levels. In response to declining devil populations, evidence for behavioural shifts was observed in spotted-tailed quolls, eastern quolls and the common brushtail possum. Over time, there is potential for behavioural changes to translate into fitness and reproductive costs or benefits which could lead to lagged changes in population size. It is essential to examine both direct predatory and indirect behavioural effects on species to understand the effects of apex predator loss on community structures (Heithaus et al. 2008). It is also necessary to note that the relative importance of behavioural effects compared with density-related effects have been questioned in recent studies (Creel and Christianson 2009, Kauffman et al. 2010), and the effects of each may be difficult to separate out. In summary, responses to apex predator decline are likely to depend on the strength of interactions between species and their perceived risk of predation, ultimately determining the magnitude of their response to apex predator loss.

6.5 Ecological restoration

The reintroduction of apex predators into terrestrial ecosystems provides evidence for the restoration of top-down control in ecosystems, with demonstrated positive effects on

biodiversity (e.g. Ripple and Beschta 2003, Fortin et al. 2005, Berger and Conner 2008). Possibly the most well studied restoration of apex predator function is the reintroduction of wolves to the Greater Yellowstone System after more than half a century of absence. Their successful reintroduction resulted in behavioural shifts in some prey species (Laundre et al. 2001) with positive effects on vegetation (Fortin et al. 2005, Ripple and Beschta 2007), and reduced density of mesopredator populations (Berger and Gese 2007) corresponding to increasing mesopredator prey populations (Berger and Conner 2008). The potential for successful restoration of ecosystems through the reintroduction of top-down control is context dependent. For example, restoring apex predators and the effective ecological function of top-down control in highly productive and anthropogenically-dominated ecosystems benefits biodiversity and protects species in lower levels of the food web; however for less productive systems, this may not be the case (Elmhagen and Rushton 2007). The strength of species interactions, environmental attributes, length of time since apex predator removal, and the social and economic conditions which may be responsible for initial apex predator extinction, may all determine the success of ecological restoration via reinstating top-down control (Ritchie et al. 2012). Implementing effective intervention strategies for ecological restoration requires extensive knowledge of ecosystem processes prior to disruption (Hobbs and Cramer 2008). Even if ecological restoration were possible, in some contexts it would be unlikely that apex predators would ever reach historical densities owing to widespread modification of habitats and continued persecution from humans (Sergio et al. 2006). As a result, while it may be possible to restore their presence, it may not be possible to restore their functional role in driving community structure and ecosystem processes (Sergio et al. 2006). Often the determinant for reintroduction success is a population viability measure for the species such as

the number of breeding pairs, however ecological factors, including species interactions and ecological function, should also be important considerations in assessing the success of reintroduction efforts (Pyare and Berger 2003).

There is potential for the reintroduction of devils into the wild, as the Tasmanian state government conservation agency maintains a large captive population both within the state and on mainland Australia. At what point in the future a viable reintroduction attempt should take place is unknown. The frequency dependent nature of the disease, where DFTD has the potential to drive devils to extinction regardless of population density (Hamede et al. 2008, McCallum et al. 2009), means that it would be futile to reintroduce devils into the wild while even low density devil populations still exist. Therefore, it may not be appropriate to consider reintroduction in Tasmania as an ecosystem conservation tool prior to disease induced extinction of wild devils. In effect it could be decades before reintroduction is an option; though isolating large areas and then the depopulation and reintroduction of devils has been proposed by the Save the Tasmanian Devil Program. This study provides answers to some of the questions posed about the ecosystem effects of devil loss, however whether some or all of these effects are reversible with the reintroduction of top-down control following a long period of absence is unknown. Given that devils were historically present on the Australian mainland, reintroduction there has been put forward as a management tool for protecting and restoring mammalian vertebrates from introduced predators (Ritchie et al. 2012). Results from this study highlight the role devils play in protecting smaller native biodiversity and suppression of feral cats indicating that this could be an effective strategy. Before reintroduction to the mainland, more research into devil ecology including den and habitat use as well as diet should be considered. The reasons for devil extinction from the mainland in the

first place and the role they may play in parallel with foxes would need to be addressed (Ritchie et al. 2012).

Re-establishing some level of top-down control may need to be considered in the immediate future to avoid irreversible ecosystem effects. Two such issues of high conservation concern which may be reduced or controlled by re-establishing top-down control are the increase in feral cat populations and the potential establishment of the red fox, the latter of which may have been unable to establish in the presence of high devil numbers. Feral cats may cause declines and ultimately the extinction of native prey species. Evidence in this thesis suggests that larger populations of this invasive species are already placing increasing pressure on small native mammals. If red foxes become established, not only will dozens of native species be at risk from fox predation, the success of any future recovery of devil populations may be diminished (Saunders et al. 2006).

The first step in assessing the viability of reintroducing devils for ecosystem stability is to determine the population density at which the devil maintains ecological function as an apex predator. The recent introduction of devils onto Maria Island, off the east coast of Tasmania (STTD Translocation Proposal) could play a key role in assessing their ecosystem effects. Devils have never been present on the island, but have been introduced to establish a free-ranging insurance population in case of extinction in the wild on mainland Tasmania. Their introduction will provide an important insight into the potential for restoration of both direct and indirect effects of top-down control. The species on Maria Island have been isolated from all mammal predators, except for feral cats, for tens of generations since their release on the island (Rounsevell 1989).

6.6 Challenges of studying large apex predators

The ability to predict and regulate the effects of apex predator loss has been hindered by a lack of appreciation of the cause of many observed ecological disruptions (Estes et al. 2011). These misunderstandings have led many to consider the evidence for apex predators' keystone role in shaping ecosystems as being exceptions limited to specific species and systems, rather than a true universal role (Terborgh et al. 2001, Estes et al. 2011). Even with widespread acknowledgement of the detrimental consequences of apex predator loss for ecosystem function and resilience, our understanding of processes that determine the strength of apex predator interactions is limited (Ritchie et al. 2012). This may in part be related to the inherent difficulty of determining the magnitude of effects attributable to apex predator decline due to common obstacles. Logistical and ethical obstacles affect many carnivore studies, which often results in inadequate controls and replication (Terborgh et al. 1999, Polis et al. 2000, Trewby et al. 2008) and can lead to ambiguous conclusions. There are few ecosystems on earth which retain intact apex predator guilds (Terborgh et al. 2001), making it challenging to study the effects of their decline and extinction retrospectively. Establishing baseline ecological data for historical ecosystems and comparative assessment may not be possible. Nevertheless, results from multiple studies at spatial scales ranging from the home range of an individual to a species entire geographic distribution and utilising different methodologies, provide consistent patterns of the effects of apex predator decline, despite some issues occurring within individual studies (Letnic et al. 2011).

There are obvious challenges to assessing the response of ecomorphologically different species across environmental gradients. For example, species responses may be confounded with environmental responses at large spatial extents. Species interact with their environment

in many ways, and the loss of apex predators will rarely occur in the absence of other interacting factors (Ritchie et al. 2012). For all broad-scale temporal and spatial studies, environmental variables and external influences should not be overlooked as potential causal factors in explaining population fluctuations of a species. Environmental variables, such as average annual rainfall, vegetation type and temperature, can vary over large spatial scales and the influence of an environmental perturbation, such as apex predator loss, may not be consistent across the entire geographic range of the species. Mesopredator populations can be influenced by human-dominated landscapes (Prange and Gehrt 2004). Consumer species can also be heavily influenced by food availability and rainfall (e.g. Owen-Smith et al. 2005). Assessing responses in a small proportion of the range of the species of interest could potentially over- or understate the population-wide species response.

Different species require different methods for detection, especially rare and cryptic species. Understanding the biology and general behaviour of a species can aid in identifying the best methods or devices to employ to answer specific questions. If the study involves multiple species, there may be a requirement to use several methods, which can add cost and time to large scale projects. Even similar-sized mesopredators with similar prey ranges, such as the feral cat and spotted-tailed quoll, may require different methods of assessment, as highlighted in this study from the efficacy of spotlighting and remote cameras for their detection. Assessing multiple species can add challenges to large-scale apex predator studies.

6.7 Directions for future research

The extensive empirical and theoretical evidence asserts that top-down control is not an anomaly limited to rare cases but is generally the consistent pattern across diverse species and

ecosystems (Terborgh et al. 2001, Estes et al. 2011). Movements away from the controversy over top-down versus bottom-up control and the requirement for independent verification in each system will prove constructive to filling the current gaps in our knowledge of both devil and global apex predator systems (Estes et al. 2011). Ecosystems are dynamic and respond continually to a multitude of environmental and biological perturbations. Studies that are conducted over long time periods and large spatial scales are a key component of future apex predator studies to determine long-term state changes caused by their decline or extinction (Ritchie et al. 2012).

For the Tasmanian ecosystem, knowing if and what changes are occurring is important for assessing the long-term environmental effects of the loss of an ecologically functional devil population and to consider the likelihood of any potential ramifications for future reintroductions for these species. Irrespective of the findings of this initial study as well as previous studies on native carnivore interactions (e.g. Jones 1997, Jones and Barmuta 1998) and assessments of other systems, particularly mainland Australia (e.g. Pickett et al. 2005, Johnson et al. 2007, Letnic et al. 2009b, Wallach et al. 2010, Kennedy et al. 2012), which comprise an array of ecologically similar native species, there are still considerable gaps in our understanding of devil's keystone role in Tasmania.

It is imperative to begin to fill these gaps as the evidence for changing food web dynamics presented in this thesis pose a real threat to biodiversity and the persistence of native fauna and flora species.

One of the significant and potentially damaging effects highlighted in this study is the increase in feral cat populations. Much of our knowledge of the effects of cats on native fauna comes

from mainland Australia, and much of it is only correlative with species declines. For species conservation in Tasmania, it would be highly beneficial to consider further the threat of cat populations to native species persistence. This could include the relationship between population size and the level of predation threat, as well as the consequences of infection with *Toxoplasma* for native species.

Internationally, there is little persuasive empirical evidence for the effects of competition between ecologically similar introduced and native carnivores, or the effect of their presence on ecosystem processes (Boitani 2001). This study touched on activity times and behaviour for top trophic predators. There would be value in initiating a more detailed and comprehensive approach to studying these changes. Further research is recommended on the interactions of the feral cat and native predator fauna. Of particular importance is how any competitive or aggressive interactions affect the cryptic spotted-tailed quoll and eastern quoll.

The different responses to devil decline of ecologically similar invasive and native species was surprising but not unexpected given the characteristics of invasive species which make them successful colonisers. Further work on how species origin influences their response to apex predator loss would be invaluable not only to the Tasmanian ecosystem but globally, as very few ecosystems lack invasive species. Further work on what a predominantly invasive system means for biodiversity, and whether this state is reversible with the reintroduction of top-down control, would also be beneficial.

The research in this thesis is focused solely on terrestrial mammalian fauna. A key aspect to extending future research efforts would be to include avian fauna, particularly the predatory birds, and also vegetation communities, scavengers and invertebrates. Some of these species

are several trophic links removed from devils, but could be influenced by cascading effects through the food web. With some notable exceptions (e.g. Berger et al. 2001, Terborgh et al. 2001, Ripple and Beschta 2006), apex predator studies rarely assess more than three links in a food web and typically follow a linear chain. Examining aspects far removed from the direct food web links to apex predators would be beneficial as other less apparent effects may be just as detrimental to the long-term viability of a species or ecosystem. A large number of bird species, including many threatened species, are prey of mesopredators and thus may suffer under increasing pressure from mesopredator populations. Possums also are known to prey on birds and bird eggs (Brown et al. 1993). Establishing the extent of secondary effects and the increasing pressure facing these species may be paramount for their long-term conservation. Avian predators including the Wedge-tailed eagle (*Aquila audax*) and scavengers, such as forest ravens (*Corvus tasmanicus*) and wasps, may also be important groups to benefit from devil decline with flow-on effects to lower levels of the food web.

Future research may need to focus more attention to the less apparent but potentially damaging consequences of apex predator loss. Disease ecology and *Toxoplasma* is one example highlighted in this study, demonstrating that the mesopredator release of cats may not just have direct predation implications for prey species, but indirect effects covering all levels of the food web via the potential increase in *Toxoplasma* transmission.

The effect of predators on ecosystems are not limited to direct lethal interactions (Lima 1998). Just the mere presence of a predator and risk of predation can have extensive effects by inducing indirect behavioural responses. Indirect effects may have a stronger influence on food web dynamics than direct lethal predation (Beckerman et al. 1997, Schmitz et al. 1997). Despite this, there is a much greater emphasis given to measures of abundance when assessing

the effects that apex predators have on other species (Ritchie et al. 2012). Behavioural responses to the loss of predator populations can occur on a much shorter timescale than demographic processes. Unfortunately there remains little evidence of how changes to an individual's anti-predator behaviour translates into fitness and reproductive potential (Lima 1998, Lind and Cresswell 2005). For future apex predator studies, assessing behavioural changes in much greater depth and scope would be advantageous. This will provide indications of apparent ecosystem changes immediately following apex predator loss, as well as an avenue for measuring the implications of behavioural changes on fitness and abundance. There needs to be greater emphasis on studies that examine indirect effects of apex predator loss as these may have greater affects on habitat utilization, reproductive potential and will inevitably lead to cascading effects through the food web.

Future research would add value to apex carnivore conservation by determining the likelihood and degree of ecological restoration that may occur following their reintroduction. Whether the reinstatement of top-down control is possible and at what point in the transition of ecosystems into new states does this become irreversible, if indeed it was in the first place, may be one of the key elements for future research. The reintroduction of top-down control may become a primary element in broad-scale conservation programs if it is possible to do so. The challenge for reintroduction of large carnivores however, may be addressing the reasons why they went extinct in the first place and these may be related to economic and social reasons (Ritchie et al. 2012). For ecosystems, where the historical apex predator is extinct, such as has occurred with the thylacine, considering other species for reintroduction who fulfil a similar functional role may be controversial, but could be worthy of consideration. The disappearance of historical native apex carnivores on mainland Australia has been linked to

the arrival of the dingo (Corbett 1995), however the presence of the dingo has been attributed to the protection of native biodiversity (Johnson et al. 2007, Letnic et al. 2009a, Letnic et al. 2009b, Wallach et al. 2009). In this respect, where original apex predators have become extinct, less emphasis should be placed on the specific apex predator species and its origins and more on their role in the ecosystem (Ritchie et al. 2012). With continued decline and extinction of apex predator, further research in these areas may yield some interesting outcomes.

6.8 Concluding remarks

This body of work contributes to the international literature on the ecosystem effects of apex predator decline and extinction through assessment of mesopredator release, behavioural shifts, invasive system states, disease transmission risks with changing ecosystem dynamics and outlines the importance of accounting for bottom-up and environmental factors in large-scale ecological studies. Invariably, there will be ecosystem changes associated with the loss of an apex predator or keystone species in any system. Determining the magnitude and scope of these effects and their cascading nature through the food-web is the real challenge. This work highlights some of the complexities associated with studying diverse ecological systems at large temporal and spatial scales. These include state-wide environmental gradients, the extinction of the thylacine and its unknown implications for the ecosystem and surrogate apex predator relationships. Despite these challenges, the culmination of evidence strongly suggests that ecosystems are transitioning into new states with significant associated threats to native biodiversity.

With the continuing spread of DFTD across the state, this may remain as one of the only comprehensive quantitative studies to have taken place while disease free regions still remain. Hence, this thesis is broad in scope with the intention of testing theories in community ecology to determine whether the loss of devils has and will cause ecosystem disruptions, and what some of the major effects on native and endangered species may be. It is by no means a comprehensive assessment of all the effects likely to be suffered in Tasmania but allows insights into some issues of pressing concern to generate wide-ranging discussion and allow future efforts to be directed into more specific research with defined outcomes. Such studies will aid in the identification of major management requirements and conservation initiatives to respond effectively to the loss of an ecologically functional devil population. Without the knowledge of ecosystem effects from the loss of the thylacine, understanding the extent of ecosystem disruption caused in the Tasmanian context by the loss of another apex predator in less than a century is crucial for biodiversity conservation.

References

1998. Rabbit Calicivirus in Tasmania Australian Bureau of Statistics, Hobart.
2009. State of the Environment Report 2009: Harvesting, control and culling of terrestrial animal species. Tasmanian State Planning Commission, Hobart.
2012. Save the Tasmanian Devil Program. Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania.
- Abbott, I. 2002. Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. *Wildlife Research* **29**:51-74.
- Abbott, I. 2006. Mammalian faunal collapse in Western Australia, 1875-1925: the hypothesised role of epizootic disease and a conceptual model of its origin, introduction, transmission, and spread. *Australian Zoologist* **33**:530-561.
- Anderson, D. R. 2001a. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* **29**:1294-1297.
- Anderson, D. R. 2003. Response to Engeman: index values rarely constitute reliable information. *Wildlife Society Bulletin* **31**:288-291.
- Anderson, M. J. 2001b. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**:32-46.
- Arundel, J. H., I. K. Barker, and I. Beveridge. 1977. Diseases of Marsupials. Pages 141-154 in B. Stonehouse and D. Gilmore, editors. *The Biology of Marsupials*. University Park Press, Baltimore.
- Attwood, H. D., P. A. Woolley, and M. D. Rickard. 1975. Toxoplasmosis in dasyurid marsupials. *Journal of Wildlife Diseases* **11**:543-551.
- Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences* **94**:10735-10738.
- Beeton, N. 2012. Population and disease modelling in the Tasmanian devil. PhD Thesis. University of Tasmania, Hobart.
- Beeton, N. and H. McCallum. 2011. Models predict that culling is not a feasible strategy to prevent extinction of Tasmanian devils from facial tumour disease. *Journal of Applied Ecology* **48**:1315-1323.
- Belcher, C. A. 1995. Diet of the Tiger Quoll *Dasyurus maculatus* in East Gippsland, Victoria. *Wildlife Research* **22**:341-357.
- Berday, M., J. P. Webster, and D. W. McDonald. 2000. Fatal attraction in rats infected with *Toxoplasma gondii*: a case of parasite manipulation of its mammalian host. *Proceedings of the Royal Society B: Biological Sciences* **267**:1591-1594.
- Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **266**:2261-2267.
- Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications* **11**:947-960.

- Berger, K. M. and M. M. Conner. 2008. Recolonizing wolves and mesopredator suppression of coyotes: Impacts on pronghorn population dynamics. *Ecological Applications* **18**:599-612.
- Berger, K. M. and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology* **76**:1075-1085.
- Berger, K. M., E. M. Gese, and J. Berger. 2008. Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn. *Ecology* **89**:818-828.
- Beschta, R. L. and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* **142**:2401-2414.
- Bettiol, S. S., D. L. Obendorf, M. Nowarkowski, and J. M. Goldsmid. 2000. Pathology of experimental toxoplasmosis in Eastern barred Bandicoots in Tasmania. *Journal of Wildlife Diseases* **36**:141-144.
- Blackhall, S. 1980. Diet of the eastern native-cat, *Dasyurus viverrinus* (Shaw), in southern Tasmania. *Australian Wildlife Research* **7**:191-197.
- Bloomfield, T. E., N. Mooney, and C. Emms. 2005. The red fox in Tasmania: an incursion waiting to happen. Proceedings of the 13th Australasian Vertebrate Pest Conference. Vertebrate Pest Committee of the Australia/New Zealand Natural Resources Management Ministerial Council, Wellington, New Zealand. .
- Blumstein, D. T. 2002. Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *Journal of Biogeography* **29**:685-692.
- Blumstein, D. T. and J. C. Daniel. 2005. The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B: Biological Sciences* **272**:1663-1668.
- Boitani, L. 2001. Carnivore introductions and invasions: their success and management options. Pages 123-144 in J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. *Carnivore Conservation*. Cambridge University Press, Cambridge, UK.
- Braithwaite, R. W. and A. D. Griffiths. 1994. Demographic variation and range contraction in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research* **21**:203-217.
- Brashares, J. S., L. R. Prugh, C. J. Stoner, and C. W. Epps. 2010. Ecological and conservation implications of mesopredator release. Pages 221-240 in J. Terborgh and J. A. Estes, editors. *Trophic cascades: Predators, prey and the changing dynamics of nature*. Island Press, Washington.
- Brook, L. A., C. N. Johnson, and E. G. Ritchie. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology* **49**:1278-1286.
- Brown, J., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* **80**:385-399.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioural Ecology and Sociobiology* **22**:37-47.
- Brown, J. S. and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**:999-1014.
- Brown, K., J. Innes, and R. Shorten. 1993. Evidence that possums prey on and scavenge birds' eggs, birds and mammals. *Notornis* **40**:169-177.

- Brown, O. J. F. 2006. Tasmanian devil (*Sarcophilus harrisii*) extinction on the Australian mainland in the mid-Holocene: multicausality and ENSO intensification. *Alcheringa: An Australasian Journal of Paleontology* **30**:49-57.
- Burnham, K. P. and D. R. Anderson. 2002. *Model Selection and Multimodal Inference: A Practical Information and Theoretic Approach*. 2nd edition. Springer-Verlag, New York.
- Byrnes, J., J. J. Stachowicz, K. M. Hultgren, A. Randall Hughes, S. V. Olyarnik, and C. S. Thornber. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecology Letters* **9**:61-71.
- Canfield, P. J., W. J. Hartley, and J. P. Dubey. 1990. Lesions of toxoplasmosis in Australian marsupials. *Journal of Comparative Pathology* **103**:159-167.
- Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. *Science* **309**:1239-1241.
- Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M. Mace. 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biology* **2**.
- Ceballos, G. and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* **296**:904-907.
- Claridge, A. W., G. Mifsud, J. Dawson, and M. J. Saxon. 2004. Use of infrared digital cameras to investigate the behaviour of cryptic species. *Wildlife Research* **31**:645-650.
- Cleaveland, S., M. K. Laurenson, and L. H. Taylor. 2001. Diseases of humans and their domestic mammals: Pathogen characteristics, host range and the risk of emergence. *Philosophical Transactions of the Royal Society B: Biological Sciences* **356**:991-999.
- Cole, R. A., D. S. Lindsay, D. K. Howe, C. L. Roderick, J. P. Dubey, N. J. Thomas, and L. A. Baeten. 2000. Biological and molecular characterizations of *Toxoplasma gondii* strains obtained from southern sea otters (*Enhydra lutris nereis*). *Journal of Parasitology* **86**:526-530.
- Corbett, L. K. 1995. *The Dingo in Australia and Asia*. University of New South Wales Press, Sydney.
- Courchamp, F., M. Langlais, and G. Sugihara. 1999. Cats protecting birds: Modelling the mesopredator release effect. *Journal of Animal Ecology* **68**:282-292.
- Cowlshaw, G. 1997. Refuge use and predation risk in a desert baboon population. *Animal Behaviour* **54**:241-253.
- Crawley, M. 2007. *The R book*. Wiley, Chichester.
- Creel, S. and D. Christianson. 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. *Ecology* **90**:2454-2466.
- Creel, S. and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology* **10**:526-538.
- Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* **307**:1959-1961.
- Crooks, K. R. and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**:563-566.

- Dalerum, F., E. Z. Cameron, K. Kunkel, and M. J. Somers. 2009. Diversity and depletions in continental carnivore guilds: Implications for prioritizing global carnivore conservation. *Biology Letters* **5**:35-38.
- Das, U. and A. K. Das. 2000. Review of canine transmissible venereal sarcoma. *Veterinary Research Communications* **24**:545-556.
- Daszak, P. 2000. Emerging infectious diseases of wildlife - Threats to biodiversity and human health (vol 287, pg 443, 2000). *Science* **287**:1756-1756.
- Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife - Threats to biodiversity and human health. *Science* **287**:443-449.
- Dawson, J. P., A. W. Claridge, B. Triggs, and D. J. Paull. 2007. Diet of a native carnivore, the spotted-tailed quoll (*Dasyurus maculatus*), before and after an intense wildfire. *Wildlife Research* **34**:342-351.
- de Castro, F. and B. Bolker. 2005. Mechanisms of disease-induced extinction. *Ecology Letters* **8**:117-126.
- Desmonts, G. and J. S. Remington. 1980. Direct agglutination test for diagnosis of Toxoplasma infection: Method for increasing sensitivity and specificity. *Journal of Clinical Microbiology* **11**:562-568.
- Dickman, C. R. 1996. Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology* **2**:185-195.
- Dickman, C. R., A. S. Glen, and M. Letnic. 2009. Reintroducing the dingo: can Australia's conservation wastelands be restored. Pages 238-269 in M. W. Haywood and M. Somers, editors. *Reintroduction of top-order predators*. Wiley-Blackwell, Oxford.
- Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution* **20**:470-474.
- Dietz, H. H., P. Henriksen, V. Bille-Hansen, and S. A. Henriksen. 1997. Toxoplasmosis in a colony of New World monkeys. *Veterinary Parasitology* **68**:299-304.
- Dobson, A. and J. Foufopoulos. 2001. Emerging infectious pathogens of wildlife. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **356**:1001-1012.
- Donnelly, C. A., R. Woodroffe, D. R. Cox, J. Bourne, G. Gettinby, A. M. Le Fevre, J. P. McInerney, and W. I. Morrison. 2003. Impact of localized badger culling on tuberculosis incidence in British cattle. *Nature* **426**:834-837.
- Driessen, M. M. and G. J. Hocking. 1992. Review and analysis of spotlight surveys in Tasmania: 1975-1990. Scientific Report 92/1, Department of Parks, Wildlife and Heritage, Tasmania.
- Driessen, M. M. and R. K. Rose. 1999. *Pseudomys higginsi*. *American Society of Mammalogists* **623**:1-5.
- Druce, D. J., J. S. Brown, G. I. H. Kerley, B. P. Kotler, R. L. Mackey, and R. O. B. Slotow. 2009. Spatial and temporal scaling in habitat utilization by klipspringers (*Oreotragus oreotragus*) determined using giving-up densities. *Austral Ecology* **34**:577-587.
- Dubey, J., P. Thulliez, R. Weigel, C. Andrews, P. Lind, and E. Powell. 1995. Sensitivity and specificity of various serologic tests for detection of Toxoplasma gondii infection in naturally infected sows. *American Journal of Veterinary Research* **56**:1030.
- Dubey, J. P. 1991. Toxoplasmosis - an overview. *The Southeast Asian journal of tropical medicine and public health* **22 Suppl**:88-92.

- Dubey, J. P. 1997. Validation of the specificity of the modified agglutination test for toxoplasmosis in pigs. *Veterinary Parasitology* **71**:307-310.
- Dubey, J. P. 2002. A review of toxoplasmosis in wild birds. *Veterinary Parasitology* **106**:121-153.
- Dubey, J. P. and C. Crutchley. 2008. Toxoplasmosis in wallabies (*Macropus rufogriseus* and *Macropus eugenii*): Blindness, treatment with atovaquone, and isolation of *Toxoplasma gondii*. *Journal of Parasitology* **94**:929-933.
- Dubey, J. P., S. T. Storandt, O. C. H. Kwok, P. Thulliez, and K. R. Kazacos. 1999. *Toxoplasma gondii* antibodies in naturally exposed wild coyotes, red foxes, and gray foxes and serologic diagnosis of toxoplasmosis in red foxes fed *T. gondii* oocysts and tissue cysts. *Journal of Parasitology* **85**:240-243.
- Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* **6**:680-687.
- Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology* **11**:624-632.
- Elmhagen, B., G. Ludwig, S. P. Rushton, P. Helle, and H. Linden. 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *The Journal of animal ecology* **79**:785-794.
- Elmhagen, B. and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? *Ecology Letters* **10**:197-206.
- Engeman, R. M. 2003. More on the need to get the basics right: population indices. *Wildlife Society Bulletin* **31**:286-287.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet earth. *Science* **333**:301-306.
- Eymann, J., C. A. Herbert, D. W. Cooper, and J. P. Dubey. 2006. Serologic survey for *Toxoplasma gondii* and *Neospora caninum* in the common brushtail possum (*Trichosurus vulpecula*) from urban Sydney, Australia. *Journal of Parasitology* **92**:267-272.
- Finke, D. L. and R. F. Denno. 2004. Predator diversity dampens trophic cascades. *Nature* **429**:407-410.
- Fisher, D. O., S. P. Blomberg, and S. D. Hoyle. 2001. Mechanisms of drought-induced population decline in an endangered wallaby. *Biological Conservation* **102**:107-115.
- Flegr, J., J. Havlicek, P. Kodym, M. Maly, and Z. Smahel. 2002. Increased risk of traffic accidents in subjects with latent toxoplasmosis: a retrospective case-control study. *BMC infectious diseases* **2**:11.
- Fleming, P., L. Corbett, R. Harden, and P. Thomson. 2001. Managing the impacts of dingoes and other wild dogs. Bureau of Rural Sciences, Canberra.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**:1320-1330.
- Fuelling, O. and S. Halle. 2004. Breeding suppression in free-ranging grey-sided voles under the influence of predator odour. *Oecologia* **138**:151-159.

- Funk, S. M., C. V. Fiorello, S. Cleavland, and M. E. Gompper. 2001. The role of disease in carnivore ecology and conservation. Pages 443-466 in J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. *Carnivore Conservation*. Cambridge University Press, Cambridge.
- Ganzhorn, J. U. 2003. Effects of introduced *Rattus rattus* on endemic small mammals in dry deciduous forest fragments of western Madagascar. *Animal Conservation* **6**:147-157.
- Gehrt, S. D. and S. Prange. 2007. Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. *Behavioral Ecology* **18**:204-214.
- Gittleman, J. L., S. Funk, D. W. Macdonald, and R. K. Wayne. 2001. Why 'carnivore conservation'? Pages 1-7 in J. L. Gittleman, S. Funk, D. W. Macdonald, and R. K. Wayne, editors. *Carnivore Conservation*. Cambridge University Press, Cambridge, U.K.
- Glen, A. S. and C. R. Dickman. 2005. Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biological Reviews* **80**:387-401.
- Glen, A. S. and C. R. Dickman. 2008. Niche overlap between marsupial and eutherian carnivores: Does competition threaten the endangered spotted-tailed quoll? *Journal of Applied Ecology* **45**:700-707.
- Glen, A. S., M. Pennay, C. R. Dickman, B. A. Wintle, and K. B. Firestone. 2011. Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology* **36**:290-296.
- Gregory, G. G. and B. L. Munday. 1976. Internal parasites of feral cats from the Tasmanian midlands and King Island. *Australian veterinary journal* **52**:317-320.
- Guiler, E. R. 1985. *Thylacine: The Tragedy of the Tasmanian Tiger*. Oxford University Press, Melbourne.
- Hamede, R. K., J. Bashford, H. McCallum, and M. Jones. 2009. Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: Using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecology Letters* **12**:1147-1157.
- Hamede, R. K., H. McCallum, and M. Jones. 2008. Seasonal, demographic and density-related patterns of contact between Tasmanian devils (*Sarcophilus harrisii*): Implications for transmission of devil facial tumour disease. *Austral Ecology* **33**:614-622.
- Harris, S. and A. Kitchener. 2005. *From forest to fjeldmark: Descriptions of Tasmania's vegetation*. Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania.
- Hartley, M. and A. English. 2005. A seroprevalence survey of *Toxoplasma gondii* in common wombats (*Vombatus ursinus*). *European Journal of Wildlife Research* **51**:65-67.
- Hartley, M. P. 2006. *Toxoplasma gondii* infection in two common wombats (*Vombatus ursinus*). *Australian veterinary journal* **84**:107-109.
- Hartley, W. J., J. P. Dubey, and D. S. Spielman. 1990. Fatal Toxoplasmosis in Koalas (*Phascolarctos cinereus*). *The Journal of Parasitology* **76**:271-272.
- Havlicek, J., Z. Gasova, A. P. Smith, K. Zvara, and J. Flegr. 2001. Decrease of psychomotor performance in subjects with latent 'asymptomatic' toxoplasmosis. *Parasitology* **122**:515-520.

- Hawkins, C. E., C. Baars, H. Hesterman, G. J. Hocking, M. E. Jones, B. Lazenby, D. Mann, N. Mooney, D. Pemberton, S. Pycroft, M. Restani, and J. Wiersma. 2006. Emerging disease and population decline of an island endemic, the Tasmanian devil *Sarcophilus harrisii*. *Biological Conservation* **131**:307-324.
- Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* **23**:202-210.
- Hesterman, H., S. M. Jones, and F. Schwarzenberger. 2008. Reproductive endocrinology of the largest dasyurids: Characterization of ovarian cycles by plasma and fecal steroid monitoring. Part I. The Tasmanian devil (*Sarcophilus harrisii*). *General and Comparative Endocrinology* **155**:234-244.
- Hill, D. E., S. Chirukandoth, and J. P. Dubey. 2005. Biology and epidemiology of *Toxoplasma gondii* in man and animals. *Animal health research reviews / Conference of Research Workers in Animal Diseases* **6**:41-61.
- Hobbs, R. J. and V. A. Cramer. 2008. Restoration ecology: Interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annual Review of Environment and Resources* **33**:39-61.
- Hocking, G. J. 1981. The population ecology of the brush-tail possum, *Trichosurus vulpecula*, in Tasmania. University of Tasmania.
- Hocking, G. J. and M. M. Driessen. 1992. Tasmanian spotlight survey manual. Department of Parks, Wildlife and Heritage, Hobart, Tasmania.
- Horwitz, P. and B. A. Wilcox. 2005. Parasites, ecosystems and sustainability: an ecological and complex systems perspective. *International Journal for Parasitology* **35**:725-732.
- Hosmer, D. W., S. Lemeshow, and S. May. 2008. *Applied Survival Analysis: Regression modeling of time-to-event data*. 2nd edition. Wiley Interscience, Hoboken, New Jersey.
- Innes, E. A. 1997. Toxoplasmosis: Comparative species susceptibility and host immune response. *Comparative Immunology, Microbiology and Infectious Diseases* **20**:131-138.
- Inskeep, W., C. H. Gardiner, R. K. Harris, J. P. Dubey, and R. T. Goldston. 1990. Toxoplasmosis in Atlantic bottle-nosed dolphins (*Tursiops truncatus*). *Journal of Wildlife Diseases* **26**:377-382.
- IUCN. 2012. IUCN Red List of Threatened Species. Version 2012.1.
- Jacob, J. and J. S. Brown. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos* **91**:131-138.
- Jennelle, C. S., E. G. Cooch, M. J. Conroy, and J. C. Senar. 2007. State-specific detection probabilities and disease prevalence. *Ecological Applications* **17**:154-167.
- Johnson, A. M., H. Roberts, and B. L. Munday. 1988. Prevalence of *Toxoplasma gondii* antibody in wild macropods. *Australian veterinary journal* **65**:199-201.
- Johnson, A. M., H. Roberts, P. Statham, and B. L. Munday. 1989. Serodiagnosis of acute toxoplasmosis in macropods. *Veterinary Parasitology* **34**:25-33.
- Johnson, C. N., J. L. Isaac, and D. O. Fisher. 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: Dingoes and marsupials in Australia. *Proceedings of the Royal Society B: Biological Sciences* **274**:341-346.
- Johnson, C. N. and S. Wroe. 2003. Causes of extinction of vertebrates during the Holocene of mainland Australia: arrival of the dingo, or human impact? *Holocene* **13**:941-948.

- Johnson, D. H. 2008. In defense of indices: the case of bird surveys. *The Journal of Wildlife Management* **72**:857-868.
- Jones, M. 1997. Character displacement in Australian dasyurid carnivores: Size relationships and prey size patterns. *Ecology* **78**:2569-2587.
- Jones, M. and T. Dayan. 2000. Foraging behavior and microhabitat use by spiny mice, *Acomys cahirinus* and *A. russatus*, in the presence of Blanford's fox (*Vulpes cana*) odor. *Journal of Chemical Ecology* **26**:455-469.
- Jones, M., Y. Mandelik, and T. Dayan. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behaviour. *Ecology* **82**:2164-2176.
- Jones, M. E. 1998. Function of vigilance in sympatric marsupial carnivores, the eastern quoll and the Tasmanian devil. *Animal Behaviour* **56**:1279-1284.
- Jones, M. E. 2003. Convergence in ecomorphology and guild structure among marsupial and placental carnivores. Pages 281-292 *in* M. E. Jones, C. R. Dickman, and M. Archer, editors. *Predators with pouches: The biology of carnivorous marsupials*. CSIRO Publishing, Melbourne, Australia.
- Jones, M. E. and L. A. Barmuta. 1998. Diet overlap and relative abundance of sympatric dasyurid carnivores: A hypothesis of competition. *Journal of Animal Ecology* **67**:410-421.
- Jones, M. E. and L. A. Barmuta. 2000. Niche differentiation among sympatric Australian dasyurid carnivores. *Journal of Mammalogy* **81**:434-447.
- Jones, M. E., M. Oakwood, C. Belcher, K. Morris, A. J. Murray, P. A. Woolley, K. B. Firestone, B. Johnson, and S. Burnett. 2003. Carnivore concerns: Problems, issues and solutions for conserving Australasia's marsupial carnivores. Pages 418-430 *in* M. E. Jones, C. R. Dickman, and M. Archer, editors. *Predators with pouches: The biology of carnivorous marsupials*. CSIRO Publishing, Melbourne.
- Jones, M. E., D. Paetkau, E. Geffen, and C. Moritz. 2004a. Genetic diversity and population structure of Tasmanian devils, the largest marsupial carnivore. *Molecular Ecology* **13**:2197-2209.
- Jones, M. E. and R. K. Rose. 1996. Preliminary assessment of distribution and habitat associations of the spotted-tailed quoll (*Dasyurus maculatus maculatus*) and eastern quoll (*D. viverrinus*) in Tasmania to determine conservation and reservation status. Nature Conservation Branch, Parks and Wildlife Service.
- Jones, M. E., G. C. Smith, and S. M. Jones. 2004b. Is anti-predator behaviour in Tasmanian eastern quolls (*Dasyurus viverrinus*) effective against introduced predators? *Animal Conservation* **7**:155-160.
- Jones, M. E. and D. M. Stoddart. 1998. Reconstruction of the predatory behaviour of the extinct marsupial thylacine. *Journal of Zoology, London* **246**:239-246.
- Jurd, R. D. 1994. "Not proper mammals": Immunity in monotremes and marsupials. *Comparative Immunology, Microbiology and Infectious Diseases* **17**:41-52.
- Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* **91**:2742-2755.
- Keesing, F., L. K. Belden, P. Daszak, A. Dobson, C. D. Harvell, R. D. Holt, P. Hudson, A. Jolles, K. E. Jones, C. E. Mitchell, S. S. Myers, T. Bogich, and R. S. Ostfeld. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* **468**:647-652.

- Kempton, H. 2010. Mice plague grips Tassie. *The Mercury Newspaper*, Hobart.
- Kennedy, M., B. L. Phillips, S. Legge, S. A. Murphy, and R. A. Faulkner. 2012. Do dingoes suppress the activity of feral cats in northern Australia? *Austral Ecology* **37**:134-139.
- Kissui, B. M. and C. Packer. 2004. Top-down population regulation of a top predator: Lions in the Ngorongoro Crater. *Proceedings of the Royal Society B: Biological Sciences* **271**:1867-1874.
- Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**:199-204.
- Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. *Proceedings of the Royal Society B: Biological Sciences* **278**:481-489.
- Lachish, S., M. Jones, and H. McCallum. 2007. The impact of disease on the survival and population growth rate of the Tasmanian devil. *Journal of Animal Ecology* **76**:926-936.
- Lachish, S., H. McCallum, D. Mann, C. E. Pukk, and M. E. Jones. 2010. Evaluation of selective culling of infected individuals to control Tasmanian devil facial tumor disease. *Conservation Biology* **24**:841-851.
- Lafferty, K. D., A. P. Dobson, and A. M. Kuris. 2006. Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America* **103**:11211-11216.
- Lafferty, K. D. and L. R. Gerber. 2002. Good medicine for conservation biology: The intersection of epidemiology and conservation theory. *Conservation Biology* **16**:593-604.
- Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: Reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* **79**:1401-1409.
- le Mar, K. and C. McArthur. 2005. Habitat selection by common brushtail possums in a patchy eucalypt-forestry environment. *Australian Mammalogy* **27**:119.
- Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. 2nd edition. Elsevier Science B.V., Amsterdam, The Netherlands.
- Leroy, E. M., P. Rouquet, P. Formenty, S. Souquiere, A. Kilbourne, J.-M. Froment, M. Bermejo, S. Smit, W. Karesh, R. Swanepoel, S. R. Zaki, and P. E. Rollin. 2004. Multiple ebola virus transmission events and rapid decline of central african wildlife. *Science* **303**:387-390.
- Letnic, M., M. S. Crowther, C. R. Dickman, and E. G. Ritchie. 2011. Demonising the dingo: how much wild dogma is enough? *Current Zoology* **57**:668-670.
- Letnic, M., M. S. Crowther, and F. Koch. 2009a. Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation* **12**:302-312.
- Letnic, M., A. Greenville, E. Denny, C. R. Dickman, M. Tischler, C. Gordon, and F. Koch. 2010. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography* **20**:343-353.
- Letnic, M., F. Koch, C. Gordon, M. S. Crowther, and C. R. Dickman. 2009b. Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B: Biological Sciences* **276**:3249-3256.
- Levi, T. and C. C. Wilmers. 2011. Wolves–coyotes–foxes: a cascade among carnivores. *Ecology* **93**:921-929.

- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* **48**:25-34.
- Lind, J. and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* **16**:945-956.
- Lindenmayer, D. B., R. D. Incoll, R. B. Cunningham, M. L. Pope, C. F. Donnelly, C. I. MacGregor, C. Tribolet, and B. E. Triggs. 1999. Comparison of hairtube types for the detection of mammals. *Wildlife Research* **26**:745-753.
- Litvaitis, J. A. and R. Villafuerte. 1996. Intraguild predation, mesopredator release, and prey stability. *Conservation Biology* **10**:676-677.
- Lodge, D. M. 1993. Biological invasions: Lessons for ecology. *Trends in Ecology and Evolution* **8**:133-137.
- MacDougall, A. S. and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**:42-55.
- Marvier, M., P. Kareiva, and M. G. Neubert. 2004. Habitat Destruction, Fragmentation, and Disturbance Promote Invasion by Habitat Generalists in a Multispecies Metapopulation. *Risk Analysis* **24**:869-878.
- McAloose, D. and A. L. Newton. 2009. Wildlife cancer: A conservation perspective. *Nature Reviews Cancer* **9**:517-526.
- McCallum, H. 2008. Tasmanian devil facial tumour disease: lessons for conservation biology. *Trends in Ecology and Evolution* **23**:631-637.
- McCallum, H. and A. Dobson. 1995. Detecting disease and parasite threats to endangered species and ecosystems. *Trends in Ecology and Evolution* **10**:190-194.
- McCallum, H., M. Jones, C. Hawkins, R. Hamede, S. Lachish, D. L. Sinn, N. Beeton, and B. Lazenby. 2009. Transmission dynamics of Tasmanian devil facial tumor disease may lead to disease-induced extinction. *Ecology* **90**:3379-3392.
- McCallum, H., D. M. Tompkins, M. Jones, S. Lachish, S. Marvanek, B. Lazenby, G. Hocking, J. Wiersma, and C. E. Hawkins. 2007. Distribution and impacts of Tasmanian devil facial tumor disease. *EcoHealth* **4**:318-325.
- McCallum, H. I. and M. E. Jones. 2012. Infectious cancers in wildlife. Pages 270-283 in A. A. Aguirre, P. Daszak, and R. S. Ostfeld, editors. *Conservation Medicine: Applied cases of ecological health*. Oxford University Press, Oxford, UK.
- McEvoy, J., D. L. Sinn, and E. Wapstra. 2008. Know thy enemy: Behavioural response of a native mammal (*Rattus lutreolus velutinus*) to predators of different coexistence histories. *Austral Ecology* **33**:922-931.
- Michalski, F. and D. Norris. 2011. Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon. *Zoologia (Curitiba)* **28**:701-708.
- Miller, M. A., I. A. Gardner, C. Kreuder, D. M. Paradies, K. R. Worcester, D. A. Jessup, E. Dodd, M. D. Harris, J. A. Ames, A. E. Packham, and P. A. Conrad. 2002. Coastal freshwater runoff is a risk factor for *Toxoplasma gondii* infection of southern sea otters (*Enhydra lutris nereis*). *International Journal for Parasitology* **32**:997-1006.
- Mills, D. J., B. Harris, A. W. Claridge, and S. C. Barry. 2002. Efficacy of hair-sampling techniques for the detection of medium-sized terrestrial mammals. I. A comparison between hair-funnels, hair-tubes and indirect signs. *Wildlife Research* **29**:379-387.

- Molsher, R., A. Newsome, and C. Dickman. 1999. Feeding ecology and population dynamics of the feral cat (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. *Wildlife Research* **26**:593-607.
- Morris, D. W., B. P. Kotler, J. S. Brown, V. Sundararaj, and S. B. Ale. 2009. Behavioral Indicators for Conserving Mammal Diversity. *Annals of the New York Academy of Sciences* **1162**:334-356.
- Morris, K. D. 2002. The eradication of the black rat (*Rattus rattus*) of Barrow and adjacent islands off the north-west coast of Australia. Pages 219-225 in C. R. Veitch and M. N. Clout, editors. *Turning the tide: the eradication of invasive species*. Proceedings of the international conference on eradication of island invasives IUCN Invasive Specialist Group, Gland Switzerland and Cambridge UK.
- Munsen, L. 2003. Scope and magnitude of disease in species conservation. in *Animal movements and disease risk: A workbook*, Costa Rica.
- Murchison, E. P. 2008. Clonally transmissible cancers in dogs and Tasmanian devils. *Oncogene* **27**:S19-S30.
- Murgia, C., J. K. Pritchard, S. Y. Kim, A. Fassati, and R. A. Weiss. 2006. Clonal origin and evolution of a transmissible cancer. *Cell* **126**:477 - 487.
- Nielsen, A. S. 2009. The potential impact of Tasmanian devil (*Sarcophilus harrisii*) decline on prey behaviour. Honours Thesis. University of Tasmania, Hobart.
- Norris, D. E., F. Michalski, and C. A. Peres. 2010. Habitat patch size modulates terrestrial mammal activity patterns in Amazonian forest fragments. *Journal of Mammalogy* **91**:551-560.
- Oakwood, M. 2000. Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology* **48**:519-539.
- Obendorf, D. L. and B. L. Munday. 1983. Toxoplasmosis in wild Tasmanian wallabies. *Australian veterinary journal* **60**:62.
- Obendorf, D. L. and B. L. Munday. 1990. Toxoplasmosis in wild eastern barred bandicoots, *Perameles gunnii*. Pages 193 - 197 in J. H. Seebeck, P. R. Brown, R. L. Wallis, and C. M. Kemper, editors. *Bandicoots and bilbies*. Surrey Beatty and Sons, Sydney.
- Obendorf, D. L., P. Statham, and M. Driessen. 1996. Detection of agglutinating antibodies to *Toxoplasma gondii* in sera from free-ranging eastern barred bandicoots (*Perameles gunnii*). *Journal of Wildlife Diseases* **32**:623-626.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist*:240-261.
- Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. *Evolutionary Ecology* **4**:220-234.
- Owen-Smith, N., D. R. Mason, and J. O. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: Density, rainfall and predation. *Journal of Animal Ecology* **74**:774-788.
- Owen, D. and D. Pemberton. 2005. *Tasmanian devil. A unique and threatened animal*. Allen & Unwin, Sydney.
- Owen, M. R. and A. J. Trees. 1998. Vertical transmission of *Toxoplasma gondii* from chronically infected house (*Mus musculus*) and field (*Apodemus sylvaticus*) mice determined by polymerase chain reaction. *Parasitology* **116**:299-304.

- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* **14**:483-488.
- Packer, C., R. D. Holt, P. J. Hudson, K. D. Lafferty, and A. P. Dobson. 2003. Keeping the herds healthy and alert: Implications of predator control for infectious disease. *Ecology Letters* **6**:797-802.
- Paine, R. T. 1980. Food Webs: Linkage, Interaction Strength and Community Infrastructure. *Journal of Animal Ecology* **49**:667-685.
- Pan, S., R. C. A. Thompson, M. E. Grigg, N. Sundar, A. Smith, and A. J. Lymbery. 2012. Western Australian marsupials are multiply infected with genetically diverse strains of *Toxoplasma gondii*. *PLoS Biology* **In Press**.
- Parameswaran, N. 2008. *Toxoplasma gondii* in Australian marsupials. Murdoch University, Perth.
- Parameswaran, N., R. M. O'Handley, M. E. Grigg, S. G. Fenwick, and R. C. A. Thompson. 2009a. Seroprevalence of *Toxoplasma gondii* in wild kangaroos using an ELISA. *Parasitology International* **58**:161-165.
- Parameswaran, N., R. M. O'Handley, M. E. Grigg, A. Wayne, and R. C. A. Thompson. 2009b. Vertical transmission of *Toxoplasma gondii* in Australian marsupials. *Parasitology* **136**:939-944.
- Parameswaran, N., R. C. A. Thompson, N. Sundar, S. Pan, M. Johnson, N. C. Smith, and M. E. Grigg. 2010. Non-archetypal Type II-like and atypical strains of *Toxoplasma gondii* infecting marsupials of Australia. *International Journal for Parasitology* **40**:635-640.
- Pearse, A.-M. and K. Swift. 2006. Transmission of devil facial-tumour disease. *Nature* **439**:549.
- Pedersen, A. B., K. E. Jones, C. L. Nunn, and S. Altizer. 2007. Infectious diseases and extinction risk in wild mammals. *Conservation Biology* **21**:1269-1279.
- Pemberton, D. 1990. Social organisation and behaviour of the Tasmanian devil, *Sarcophilus harrisii*. PhD Thesis. University of Tasmania, Hobart, Tasmania.
- Pickett, K. N., D. S. Hik, A. E. Newsome, and R. P. Pech. 2005. The influence of predation risk on foraging behaviour of brushtail possums in Australian woodlands. *Wildlife Research* **32**:121-130.
- Polis, G. A. and R. D. Holt. 1992. Intraguild predation: The dynamics of complex trophic interactions. *Trends in Ecology & Evolution* **7**:151-154.
- Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* **15**:473-475.
- Prange, S. and S. D. Gehrt. 2004. Changes in mesopredator-community structure in response to urbanization. *Canadian Journal of Zoology* **82**:1804-1817.
- Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. *BioScience* **59**:779-791.
- Purvis, A., M. Cardillo, R. Grenyer, and B. Collen. 2005. Correlates of extinction risk: phylogeny, biology, threat and scale. Pages 295-316 in A. Purvis, J. L. Gittleman, and T. Brooks, editors. *Phylogeny and Conservation*. Cambridge University Press.
- Purvis, A., J. L. Gittleman, G. Cowlshaw, and M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* **267**:1947-1952.
- Purvis, A., G. M. Mace, and J. L. Gittleman. 2001. Past and future carnivore extinctions: a phylogenetic perspective. Pages 11-34 in J. L. Gittleman, S. Funk, D. W. Macdonald,

- and R. W. Wayne, editors. *Carnivore Conservation*. Cambridge University Press, Cambridge.
- Pyare, S. and J. Berger. 2003. Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves. *Biological Conservation* **113**:63-73.
- Raberg, L., A. L. Graham, and A. F. Read. 2009. Decomposing health: tolerance and resistance to parasites in animals. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**:37-49.
- Reale, D. and M. Festa-Bianchet. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour* **65**:463-470.
- Recher, H. F. and L. Lim. 1990. A review of current ideas of the extinction, conservation and management of Australia's terrestrial vertebrate fauna. *Proceedings of the Ecological Society of Australia*:287-301.
- Remington, J. S., P. Thulliez, and J. G. Montoya. 2004. Recent developments for diagnosis of toxoplasmosis. *Journal of Clinical Microbiology* **42**:941.
- Rhodes, J. R., T. Wiegand, C. A. McAlpine, J. Callaghan, D. Lunney, M. Bowen, and H. P. Possingham. 2006. Modeling species' distributions to improve conservation in semiurban landscapes: Koala case study. *Conservation Biology* **20**:449-459.
- Ripple, W. J. and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* **184**:299-313.
- Ripple, W. J. and R. L. Beschta. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation* **133**:397-408.
- Ripple, W. J. and R. L. Beschta. 2007. Restoring Yellowstone's apsen with wolves. *Biological Conservation* **138**:514-519.
- Ripple, W. J. and R. L. Beschta. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation* **141**:1249-1256.
- Ritchie, E. G., B. Elmhagen, A. S. Glen, M. Letnic, G. Ludwig, and R. A. McDonald. 2012. Ecosystem restoration with teeth: what role for predators? *Trends in Ecology and Evolution* **27**:265-271.
- Ritchie, E. G. and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**:982-998.
- Roemer, G. W., M. E. Gompper, and B. V. Valkenburgh. 2009. The ecological role of the mammalian mesocarnivore. *BioScience* **59**:165-173.
- Rogers, C. M. and M. J. Caro. 1998. Song sparrows, top carnivores and nest predation: A test of the mesopredator release hypothesis. *Oecologia* **116**:227-233.
- Rounsevell, D. 1989. Managing offshore island reserves for nature conservation in Tasmania. Pages 157-161 in A. Burbidge, editor. *Australian and New Zealand islands: Nature conservation values and management*. Department of Conservation and Land Management.
- Rounsevell, D. E., R. J. Taylor, and G. J. Hocking. 1991. Distribution records of native terrestrial mammals in Tasmania. *Wildlife Research* **18**:699-717.
- Salo, P., E. Korpimäki, P. B. Banks, M. Nordstrom, and C. R. Dickman. 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B-Biological Sciences* **274**:1237-1243.

- Sansom, A., J. Lind, and W. Cresswell. 2009. Individual behavior and survival: the roles of predator avoidance, foraging success, and vigilance. *Behavioral Ecology* **20**:1168-1174.
- Sarre, S. D., A. J. MacDonald, C. Barclay, G. R. Saunders, and D. S. L. Ramsey. 2012. Foxes are now widespread in Tasmania: DNA detection defines the distribution of this rare but invasive carnivore. *Journal of Applied Ecology* **In Press**.
- Saunders, G., C. Lane, S. Harris, and C. R. Dickman. 2006. Foxes in Tasmania: a report on the incursion of an invasive species. Invasive Animals Cooperative Research Centre, Canberra.
- Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* **78**:1388-1399.
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. *American Naturalist* **155**:141-153.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**:153-163.
- Schmitz, O. J. and K. B. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. *Ecology* **82**:2072-2081.
- Schrag, S. J. and P. Wiener. 1995. Emerging infectious disease: what are the relative roles of ecology and evolution? *Trends in Ecology and Evolution* **10**:319-324.
- Scott, M. E. 1988. The Impact of Infection and Disease on Animal Populations: Implications for Conservation Biology. *Conservation Biology* **2**:40-56.
- Sergio, F., I. A. N. Newton, L. Marchesi, and P. Pedrini. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* **43**:1049-1055.
- Shepherd, N. C. and I. T. Mahood. 1978. The potential effect of feral dogs and cats on Australian native fauna. *Australian Advances in Veterinary Science*:108.
- Short, J. and A. Smith. 1994. Mammal decline and recovery in Australia. *Journal of Mammalogy* **75**:288-297.
- Smith, A. P. and D. G. Quin. 1996. Patterns and causes of extinctions and decline in Australian conilurine rodents. *Biological Conservation* **77**:243-267.
- Soulé, M. E., D. T. Bolger, C. A. Allison, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* **2**:75-92.
- Southwell, C. and M. Fletcher. 1993. Repeatability and standardisation of roadside spotlight counts of mammals in Tasmania. *Australian Mammalogy* **16**:73-75.
- Stokes, V. L., P. B. Banks, R. P. Pech, and D. M. Spratt. 2009. Competition in an invaded rodent community reveals black rats as a threat to native bush rats in littoral rainforest of south-eastern Australia. *Journal of Applied Ecology* **46**:1239-1247.
- Taylor, J. M. and J. H. Calaby. 1988. *Rattus lutreolus*. *American Society of Mammalogists* **299**:1-7.
- Taylor, R. J. 1985. Identification of the hair of Tasmanian mammals. *Papers and Proceedings of the Royal Society of Tasmania* **119**:69-82.
- Terborgh, J., J. A. Estes, P. Paquet, K. Ralls, D. Boyd-Heiger, B. J. Miller, and R. F. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. *Continental Conservation: Scientific Foundations of Regional Reserve Networks*.

- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**:1923-1926.
- Thomas, F., K. D. Lafferty, J. Brodeur, E. Elguero, M. Gauthier-Clerc, and D. Misse. 2012. Incidence of adult brain cancers is higher in countries where the protozoan parasite *Toxoplasma gondii* is common. *Biology Letters* **8**:101-103.
- Thompson, R. C. A., A. J. Lymbery, and A. Smith. 2010. Parasites, emerging disease and wildlife conservation. *International Journal for Parasitology* **40**:1163-1170.
- Thorne, E. T. and E. S. Williams. 1988. Disease and endangered species: The black-footed ferret as a recent example. *Conservation Biology* **2**:66-74.
- Torrey, E. F. and R. H. Yolken. 2003. *Toxoplasma gondii* and Schizophrenia. *Emerging Infectious Diseases* **9**:1375-1380.
- Trewby, I. D., G. J. Wilson, R. J. Delahay, N. Walker, R. Young, J. Davison, C. Cheeseman, P. A. Robertson, M. L. Gorman, and R. A. McDonald. 2008. Experimental evidence of competitive release in sympatric carnivores. *Biology Letters* **4**:170-172.
- Triggs, B., H. Brunner, and E. P. Ltd. 2002. Hair ID: An interactive tool for identifying Australian mammalian hair. CSIRO Publishing.
- van Dyck, S. and R. Strahan, editors. 2008. *Mammals of Australia*. New Holland Press.
- Vance-Chalcraft, H. D., J. A. Rosenheim, J. R. Vonesh, C. W. Osenberg, and A. Sih. 2007. The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology* **88**:2689-2696.
- Wallach, A. D., C. N. Johnson, E. G. Ritchie, and A. J. O'Neill. 2010. Predator control promotes invasive dominated ecological states. *Ecology Letters* **13**:1008-1018.
- Wallach, A. D., B. R. Murray, and A. J. O'Neill. 2009. Can threatened species survive where the top predator is absent? *Biological Conservation* **142**:43-52.
- Webster, J. P. 1994. The effect of *Toxoplasma gondii* and other parasites on activity levels in wild and hybrid *Rattus norvegicus*. *Parasitology* **109**:583-589.
- Webster, J. P. 2001. Rats, cats, people and parasites: the impact of latent toxoplasmosis on behaviour. *Microbes and Infection* **3**:1037-1045.
- While, G. M. and C. McArthur. 2006. Distance from cover affects artificial food-patch depletion by macropod herbivores. *Wildlife Research* **33**:565-570.
- Wilson, G. J. and R. J. Delahay. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research* **28**:151-164.
- Woinarski, J. C. Z., S. Legge, J. A. Fitzsimons, B. J. Traill, A. A. Burbidge, A. Fisher, R. S. C. Firth, I. J. Gordon, A. D. Griffiths, and C. N. Johnson. 2011. The disappearing mammal fauna of northern Australia: context, cause, and response. *Conservation Letters* **4**:192-201.
- Woodroffe, R. 1999. Managing disease threats to wild mammals. *Animal Conservation* **2**:185-193.
- Wroe, S. and C. N. Johnson. 2003. Bring back the devil? *Nature Australia* **27**:84.
- Wroe, S., C. McHenry, and J. Thomason. 2005. Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society B-Biological Sciences* **272**:619-625.
- Young, T. P. 1994. Natural die-offs of large mammals: implications for conservation. *Conservation Biology* **8**:410-418.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science+Business, New York.



The End

© Kris Carlyon, 2010